

A taxonomic revision of the family Oncopodidae I. New genera and new species of *Gnomulus* Thorell (Opiliones, Laniatores)

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A taxonomic revision of the family Oncopodidae I. New genera and new species of *Gnomulus* Thorell (Opiliones, Laniatores). - The genera *Oncopus* Thorell, 1876 and *Gnomulus* Thorell, 1890 are rediagnosed; *Pelitus* Thorell, 1891 is synonymised with *Gnomulus* because of intermediate forms and identical penis structure. Seventeen species described under *Pelitus* are transferred to *Gnomulus*; generic placement in six of them (known only from females or juveniles) is provisional. Taxonomic characters of Oncopodidae and relationships within the Oncopodidae and with other families are discussed. *Pelitus thorelli* Schwendinger, 1992 is a primary homonym; the species unduely described under this name is transferred to *Gnomulus* and renamed *G. baharu* Schwendinger nom. n. Three new genera and thirteen new species of mostly small oncopodid opilionids are described. *Palaeoncopus* gen. n., with *P. gunung* sp. n., *P. kerdil* sp. n., *P. katik* sp. n. from Sumatra possess a short, distad-directed, non-expandable glans penis, which is considered plesiomorphic. *Biantoncopus* gen. n., with *B. fuscus* sp. n. from the Philippines, has a similar but expandable glans. This character is regarded as apomorphic. Seven new species are placed in *Gnomulus*, i. e. *G. crucifer* sp. n., *G. maculatus* sp. n., *G. coniceps* sp. n., *G. leyteensis* sp. n., *G. laruticus* sp. n., *G. asli* sp. n. and *G. hirsutus* sp. n. Their penis morphology, with a short proximad-directed glans, is typical for most Oncopodidae (also present in *Oncopus*) and is considered derived from the *Palaeoncopus*-type. *Caenoncopus* gen. n., including *C. tenuis* sp. n., *C. affinis* sp. n. and *C. cuspidatus* (Schwendinger) comb. n. (transferred from *Oncopus*) from Sumatra, has a glans penis comprising a strongly elongated, proximad-directed stylus wrapped in a membraneous collar. This structure appears highly apomorphic and is possibly an extreme modification of the penis type in *Gnomulus* and *Oncopus*. Intermediate states of reduction of glans sclerites and enlargement of stylus are present in *G. crucifer* sp. n. and *G. maculatus* sp. n.,

though they probably belong to a different evolutionary lineage. Four penis types are distinguished for the Oncopodidae; their evolution, generic significance and functional morphology are discussed.

Key-words: Opiliones - Oncopodidae - Taxonomy - Penis morphology - Evolution - SE Asia.

INTRODUCTION

Since a revisional study on the Oncopodidae of the Natural History Museum of Geneva (SCHWENDINGER 1992), extensive and exceptionally rich new material has become available from the collections of various colleagues and ourselves. Several of the small specimens in this material are particularly interesting, as they look similar to the enigmatic *Oncopus cuspidatus* Schwendinger, which has no genital-morphological resemblance to other Oncopodidae or even to other opilionids previously known. After close examination, surprisingly they turned out to include not only close relatives of *O. cuspidatus* but also other forms with unexpected penis morphology. An account of this remarkable new material is given here; a thorough revision of the remaining taxa with new descriptions shall follow in subsequent papers. Although the newly available material contains plenty of exceptional forms, it nevertheless originates from quite sporadic samplings and we believe that it only represents the tip of an iceberg. With more systematic sampling by sifting and soil extraction in all parts of Southeast Asia, a plethora of small and inconspicuous oncopodid taxa is expected to be discovered.

Abbreviations and terms used in the text: CCD collection of C. Deeleman-Reinhold, Sparrenlaan; MAR collection of J. Martens, Mainz; MCSNG Museo Civico di Storia Naturale, Genova; MHNG Muséum d'histoire naturelle, Genève; SMF Senckenberg Museum, Frankfurt; ZMA Zoological Museum, University of Amsterdam; ZMT Zoological Museum, University of Turku. Body measurements refer to the length of the dorsal scutum (i.e. distance between anterior margin of carapace and posterior margin of abdominal part of dorsal scutum). Leg articles were measured on their dorsal side, from joint to joint. All measurements are given in mm.

TAXONOMIC REMARKS

SPECIES CONCEPT

We tried to find characters for distinctions and relationships between species in their penis morphology, but faced the problem of where to draw the boundaries in regard to the biospecies concept. Allopatric, morphologically similar and obviously closely related populations needed to be divided into "biospecies", without knowing whether or not reproductive isolation exists. As empirical data for such a grouping in Oncopodidae are non-existent (see MARTENS 1978 for Biantidae), we had to draw species boundaries in an arbitrary manner. Each seemingly allopatric population with

clear morphological distinctiveness is here regarded as a separate species. Due to the scattered and very localized nature of Oncopodidae collections (formerly caused by restricted accessibility, today by habitat destruction), individual finds may show morphological distinctiveness, which does not correspond with species identity in the sense of the biospecies concept. In addition, geographical variation in Oncopodidae remains largely unclear. Therefore the species concept necessarily used here is close to the phylogenetical species concept, which clusters diagnosable populations into so-called "phylopecies" (ZINK 1997).

TRADITIONAL SYSTEM AND GENERIC LIMITS

THORELL (1876) described the subfamily Oncopodinae (under the family Cosmetoidae Koch) and later (1890) upgraded them to family rank. Within this group he successively distinguished three genera: *Oncopus* (Thorell, 1876), *Gnomulus* (Thorell, 1890) and *Pelitus* (Thorell, 1891), which remained valid until the present day. The distinction between these genera is essentially based on tarsal formula (*Oncopus* 1-1-1-1, *Gnomulus* and *Pelitus* 2-2-3-3) and presence (*Pelitus*) or absence (*Gnomulus*) of an oblique, strong, triangular eye tubercle (THORELL 1891: 93 - "Oculi basi tuberculi transversi fortis trianguli impositi."). The latter character, however, shows all transitions from a plane interocular area to a rounded hump and an acutely pointed prorect or erect eye tubercle in both nominal genera. The interocular area is sexually dimorphic in some species, with a low eye tubercle present in ♀♀ and absent in ♂♂. This was shown for *G. lannaianus* (sub *Pelitus lannaianus*, SCHWENDINGER 1992) and also occurs in *G. sumatranus* (in preparation). Therefore the traditional distinction between *Gnomulus* and *Pelitus* cannot be maintained. Penis morphology in both genera (first illustrated for *Gnomulus* by LOMAN 1903: fig. 5f) is of the same type. A detailed account of this shall be given in our next paper.

In contemporary taxonomy of arthropods ♂ genitalia are regarded to be among the most informative characters explaining relationships between taxa. Within the last decades this view became generally accepted and brought forth significant changes to high level systematics of opilionids. On the base of the genital morphology of ♂♂, the family Fissiphallidae was established recently (MARTENS 1988) and the traditional suborders Cyphophthalmi and Palpatores were united to one suborder Cyphopalpatores (MARTENS 1980, 1986). Applying the same criteria to the family Oncopodidae, we place *Pelitus* in synonymy with *Gnomulus*, as was already suggested by LOMAN (1902: 183). Three new genera with penis morphology distinctly different from *Gnomulus* and *Oncopus* are established in the following.

DEFINITION OF THE FAMILY ONCOPODIDAE

Oncopodid harvestmen are readily distinguishable by external characters, but most of these seem to be plesiomorphic for opilionids and are therefore not appropriate to define the family. This holds true for the following characters in particular:

extensive dorsal scutum (carapace and abdominal tergites fused); low number (1-3) of tarsal articles; restricted unidirectional articulation of the legs and pedipalps. The large, fused dorsal scutum clearly distinguishes the Oncopodidae from other Laniatores, but similar structures are also found in the Sironoidea and the Trogulidae, which are likewise slow-moving, soil-dwelling opilionids. All three taxa are additionally characterized by a low number of tarsal articles (up to 2 in Sironoidea ♂♂, up to 4 in Trogulidae and up to 3 in Oncopodidae). Obviously the state of both characters is correlated with the mode of life of these cryptic animals. In Sironoidea large dorsal scutum and few tarsalia are considered plesiomorphic, whereas in the taxonomically distant Trogulidae the same most likely represent apomorphic reversals. Though oncopodids already possess clearly derived genital characters (e.g. hemolymph-pressure penis), their large scutum and low number of tarsalia are difficult to evaluate. We assume that they represent plesiomorphies.

Only the following three character states are presently regarded as autapomorphic of the Oncopodidae, defining the family as a monophyletic group:

1. Glans penis with lateral sclerites fused by an intermediate (median) plate (Figs 1, 134). In other families, symmetrical glans structures are not interconnected and can be moved independently from each other (MARTENS 1986).

2. Ovipositor laterally compressed, not dorso-ventrally flattened or circular in cross-section (MARTENS *et al.* 1981). This trait holds true not only for *Oncopus* (MARTENS *et al.* 1981), but was also found in *Gnomulus*, *Biantoncopus* gen. n., *Palaeoncopus* gen. n. and *Caenoncopus* gen. n. In the smallest representatives, however, ovipositor cross-sections generally tend to be more roundish.

3. Cuticular appendages (paired or unpaired) on the carapace and the first abdominal tergite, respectively, form a small "bridge". This character is found only in Oncopodidae (ŠILHAVÝ 1960).

Regarding the scarcity of derived characters identified by now, the taxonomic position of the family Oncopodidae is again open to question. By no means can we presently trace character states that may warrant the status of a superfamily or a similarly high-ranking taxon for the Oncopodidae alone, as was suggested earlier (ŠILHAVÝ 1960, MARTENS *et al.* 1981). At the present state of knowledge no sister group can be identified for the Oncopodidae.

DESCRIPTIONS

Caenoncopus gen. n.

Diagnosis: Distinguished by penis with dorso-ventrally depressed truncus, basally bilobed, subbasally not constricted; subapical glans large, composed of a strongly elongated, cylindrical stylus proximally enclosed in a membranous collar; tip of stylus asymmetrical; glans folded proximad in resting position, lying in a shallow trench on the dorsal surface of the truncus. Body small without elevated scutal areas; interocular area developed as a round hump, not abruptly separated from

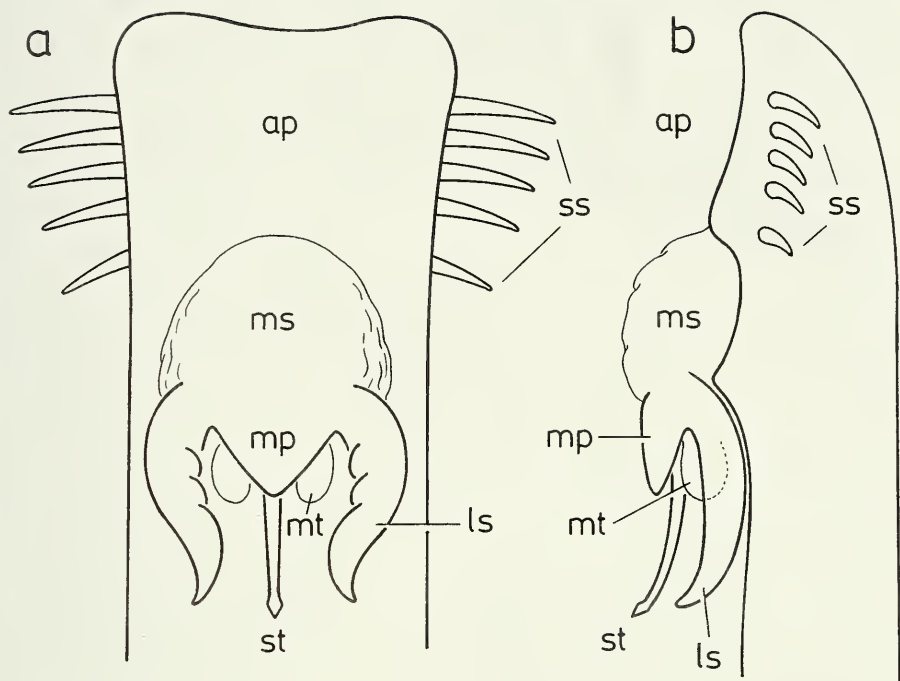


FIG. 1

General scheme of an oncopodid penis of the *Gnomulus/Oncopus* type; ventral (a) and lateral (b) view of distal part. - Apex of truncus (ap); two lateral sclerites (ls); median plate (mp); membraneous socket (ms); two membraneous tubes (mt); subapical setae (ss); stylus (st).

low thoracic area; chelicerae small, weak, with a pronounced dorso-distal and a small ventro-median hump on proximal article, no modifications on chelical hand; pedipalps with small ventral processes on proximal femur and trochanter; ventral coxa II with antero-proximal process; legs 3142, tarsal formula 1-1-2-2 or 1-1-3-3. External sexual dimorphism in shape of palpal trochanter or absent.

Etymology: Greek: *kainos* = new, young; *oncos* = swelling; *podos* = foot; male gender. The Latinized name (correctly spelled "Caenooncopus", one "o" omitted to make it more euphonious) refers to the highly derived genital morphology of this genus and to its relationship with *Oncopus*.

Type species: *Oncopus cuspidatus* Schwendinger.

Species account and distribution: Three apparently allopatric species, i.e. *C. cuspidatus* comb. n., *C. tenuis* sp. n., *C. affinis* sp. n., are known from Sumatra. The latter two species occur in close proximity and are also closest relatives.

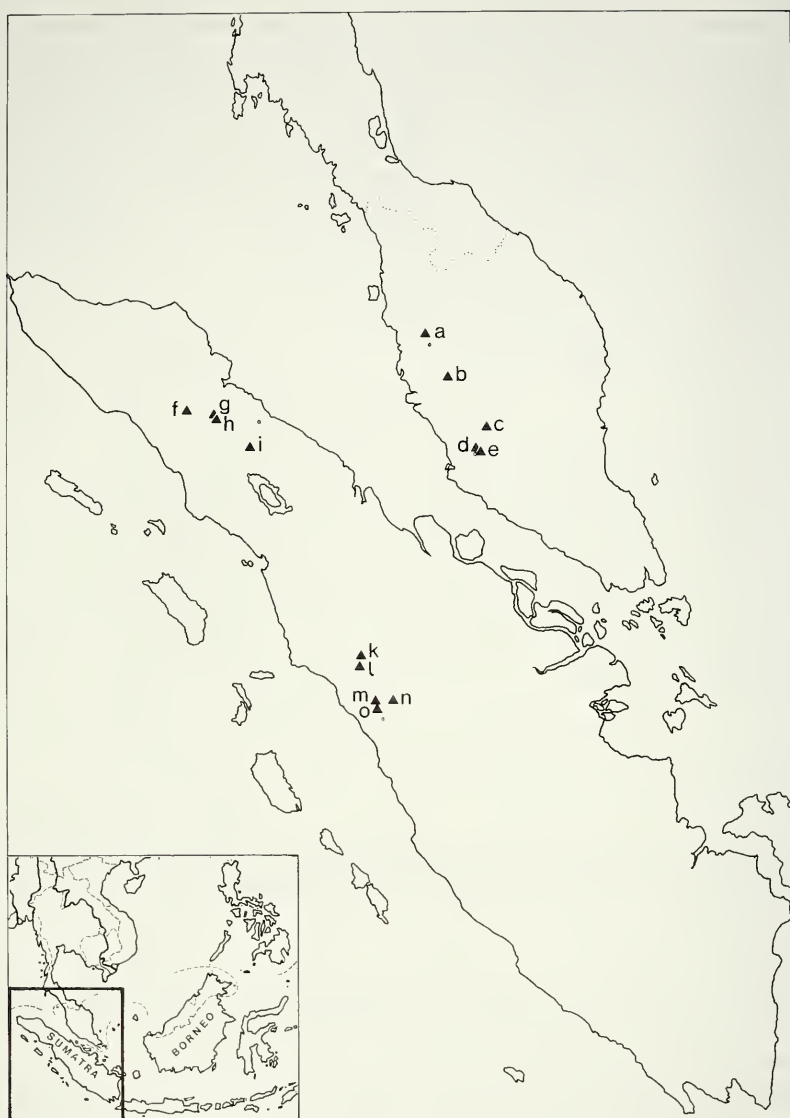


FIG. 2

Distribution of Oncopodidae in the Malay Peninsula and Sumatra. Only localities of species treated in this paper are shown. - a) Maxwell Hill (*Gnomulus laruticus* sp. n.); b) Chenderiang (*G. asli* sp. n.); c) road to Genting Highlands (*G. hirsutus* sp. n.); d) Templer Park (*G. hirsutus* sp. n.); e) Ulu Gombak (*G. hirsutus* sp. n.); f) Ketambe (*Caenoncopus cuspidatus*, *Palaeoncopus kerdil* sp. n.); g) Bukit Lawang (*C. cuspidatus*); h) Bohorok [Langkat Reserve] (*C. cuspidatus*, *P. katik* sp. n.); i) road Brastagi - Sibolangit [Deli Serdang] (*C. cuspidatus*); k) Pantí (*C. affinis* sp. n.); l) road Lubuksikaping - Pantí (*C. affinis* sp. n.); m) Palopo Nature Reserve (*C. tenuis* sp. n.); n) 5 km SE of Payakumbuh (*C. tenuis* sp. n.); o) Mt. Singgalang (*P. gunung* sp. n.).



FIG. 3

Distribution of Oncopodidae in the Philippines. Only localities of species treated in this paper are shown. - a) Sagada (*Gnomulus maculatus* sp. n.); b) Baguio, Cristal Cave (*G. coniceps* sp. n.); c) Mt. Santo Thomas (*G. crucifer* sp. n.); d) Puerto Galera (*G. maculatus* sp. n.), doubtful record; e) Lake Danao, Leyte (*Biantoncopus fuscus* sp. n.); f) Visca N of Baybay (*B. fuscus* sp. n., *G. leyteensis* sp. n.).

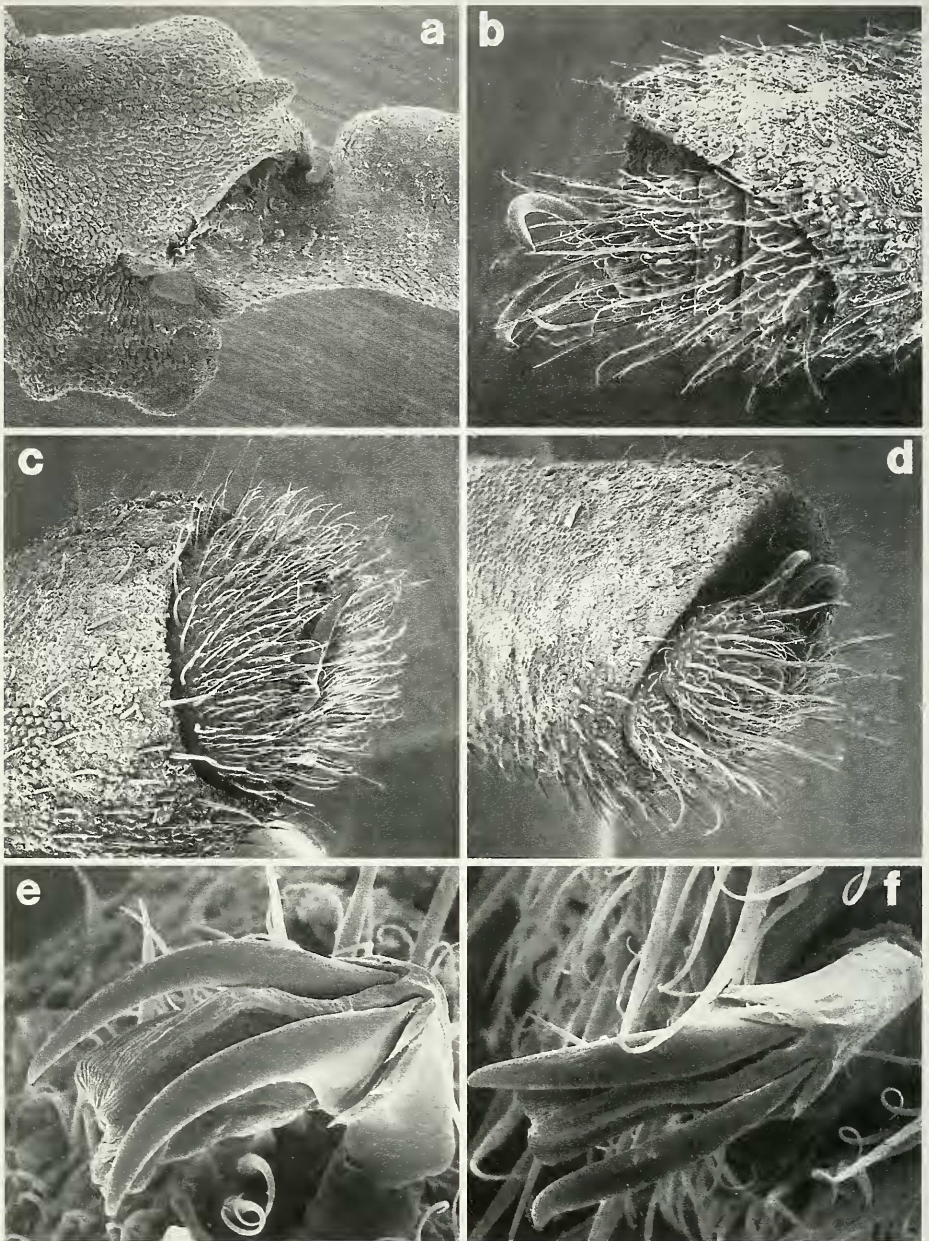


FIG. 4. Scanning electron micrographs showing external characters of Oncopodidae species. - a) *Palaeoncopus gunung* sp. n., left ♀ palpal trochanter and base of femur, prolateral view; b) *Caenoncopus tenuis* sp. n., tarsus and distal part of metatarsus IV; c-f) *C. cuspidatus* (Schwendinger), tarsus and distal part of metatarsus of leg II (c) and leg IV (d), claws and arolium on leg IV of juvenile (e-f).

Caenoncopus cuspidatus (Schwendinger) comb. n.

Figs 4c-f, 5a-d, 6-8

Oncopus cuspidatus Schwendinger, 1992: 190-192, figs. 67-80. Description of ♂.

Types: SUMATRA, Northern Sumatra Province, Langkat, Bukit Lawang Nature Reserve, 180 m, ♂ holotype (MHNG Sum-85/49). - Deli Serdang, north of Brastagi, 1400 m, ♂ paratype (MHNG Sum-85/47); both leg. B. Hauser, 8.-20.XI.1985.

New material: SUMATRA, Aceh Province, Mt. Leuser National Park, Ketambe Research Station, 300-500 m, 23.-30.XI.1989, 4 ♂, 13 ♀; 800 m, 28.XI.1989, 1 ♀; all leg. D. Agosti, I. Löbl & D. Burckhardt (MCSNG, MHNG). - North Sumatra Province, Langkat, Bukit Lawang Nature Reserve, 11.-12.X.1990, 1 ♂, 1 ♀; leg. A. Riedel (MAR). - Bohorok, 7.VIII.1982, 1 ♂, 1 ♀, 13.XI.1983, 1 ♀, 30.XII.1993, 2 ♀; all leg. C. Deeleman-Reinhold & P. Deeleman (CCD). - Langkat, Bukit Lawang Nature Reserve, Bohorok river, 5.VII.1984, 1 ♂, 2 ♀; leg. J. Robert (MHNG). - Forest 7 km north of Brastagi, 1500 m, 2.XII.1989, 1 ♂, 6 ♀; all leg. D. Agosti, I. Löbl & D. Burckhardt (MHNG).

Diagnosis (extended): Relatively large species; scuta smooth, with characteristic pattern; palpal femur with ventro-basal process (Figs 7, 8); palpal trochanter sexually dimorphic, with distinct ventral process only in ♀♀ (Fig. 7); tarsal formula 1-1-2-2; genital operculum with anterior hump (Fig. 6). Truncus penis with rounded apex drawn into an obtuse angle, bearing two widely separated rows of subapical setae on each side; stylus very long, almost reaching base of truncus, wrapped in a membraneous collar almost throughout its entire length; apex of stylus free, corkscrew-shaped (Fig 5a-d, SCHWENDINGER 1992: figs 74-80).

Remark: The small proximal tarsalia on the posterior legs, partly overlapped by the terminal edge of the metatarsus (Fig. 4d), were not recognized in the original description. Therefore *C. cuspidatus* was placed in the genus *Oncopus*. However, this placement was provisional. The author was aware of the uniqueness of the species, but decided not to establish a new genus because of the sparse material (2 ♂) available (SCHWENDINGER 1992: 197).

Variation: Measurements range: ♂: body length 3.65-4.51 (\bar{x} = 4.09, SD = 0.274), width 2.08-2.68 (\bar{x} = 2.44, SD = 0.193), n = 10; ♀: body length 3.59-4.39 (\bar{x} = 4.05, SD = 0.238), width 2.07-2.85 (\bar{x} = 2.40, SD = 0.187), n = 27. Body size gradually decreases in between the three populations.

Population:	mean ♂ body length (SD)	mean ♀ body length(SD):
Ketambe	4.37 (0.089), n = 4	4.24 (0.090), n = 14
Bukit Lawang and env.	4.02 (0.056), n = 4	3.98 (0.052), n = 7
Brastagi and environs	3.67 (0.015), n = 2	3.68 (0.049), n = 6

Distribution (Fig. 2): Known from the southern part of Aceh Province and from the northern part of North Sumatra Province. The specimens examined originate from three separate areas: 1. Ketambe; 2. Bukit Lawang Reserve, Bohorok, Langkat; 3. Brastagi, Deli Serdang.

Bionomics: The specimens were collected from the leaf litter of a lowland rain forest and a montane rain forest with various degrees of disturbance.

Caenoncopus tenuis sp. n.

Figs 4b, 9-17

Material: SUMATRA, West Sumatra Province, 5 km southeast of Payakumbuh, 600 m, ♂ holotype (MHNG), 9 ♂, 4 ♀ paratypes (MAR, MCSNG, MHNG), 20.-21.XI.1989. - Palopo Nature Reserve, north of Bukittinggi, 900 m, 1 ♂ paratype (MHNG), 18.-20.XI.1989. All specimens leg. D. Agosti, I. Löbl & D. Burckhardt.

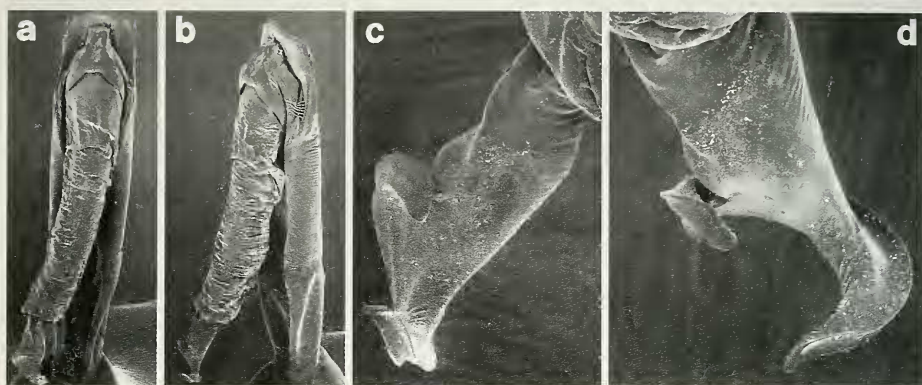
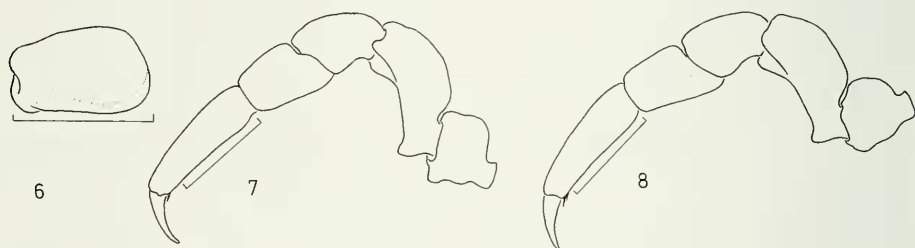


FIG. 5

Scanning electron micrographs of penis of *Caenoncopus cuspidatus* (Schwendinger): total penis, dorsal (a) and lateral (b) view; apex of glans, fronto-dorsal (c) and dorso-distal view (d).



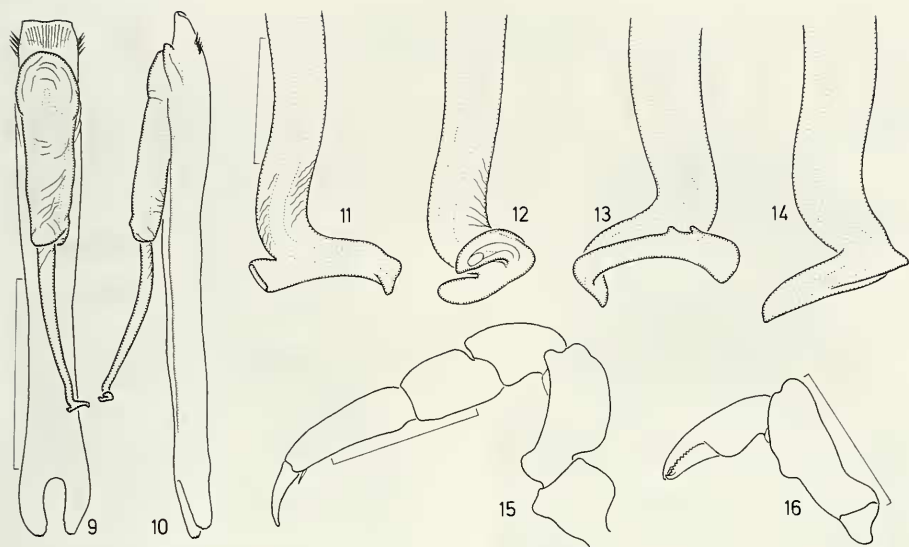
FIGS 6-8

Caenoncopus cuspidatus (Schwendinger): ♂ holotype (8), ♀ (6, 7). - Genital operculum, latero-ventral view (6); left palp, retrolateral view (7, 8). - Scale lines 0.5 mm.

Etymology: Latin: *tenuis* = small, thin, delicate.

Diagnosis: Closely related to *C. cuspidatus*, distinguished by smaller size and less extensive dark patches on dorsal and ventral scuta; distinct ventral process on palpal trochanter also present in ♂♂; tarsal formula 1-1-3-3; genital operculum without anterior hump. Truncus penis with broadly truncate apex carrying only one short row of subapical lateral setae on each side; stylus shorter, not reaching base of truncus; membraneous collar enclosing only basal half of stylus; apex of stylus different in shape (Figs 9-14).

Description: ♂ (holotype). Coloration: Body mostly light amber, except for: dark reticulation on carapace, dark margin and transverse bands on abdominal part of dorsal scutum (Fig. 17a), widely separated lateral pairs of dark transverse patches on



FIGS 9-16

Caenoncopus tenuis sp. n.; ♂ holotype (9-12), ♂ paratype (13-14), ♀ paratype (15-16). - Penis, dorsal (9) and lateral view (10); apex of stylus, dorsal (11), lateral (12), ventral (13) and contra-lateral view (14); left palp, retrolateral view (15); left chelicera, retrolateral view (16). - Scale lines 0.05 mm (11-14), 0.5 mm (9-10, 15-16).

ventral scutum (Fig. 17b). Genital operculum, process on coxae II and proximal zone of tibiae I, II and metatarsus II darkened.

Carapace short, interocular area a low hump; dorsal and ventral scuta smooth, without furrows or elevations (Figs 17a, c). Distinct antero- and postero-proximal processes on coxa II, two smaller sub-proximal and median processes on coxa I. Genital operculum relatively large (Fig. 17b).

Chelicerae (Fig. 16) small; proximal article with distinct dorso-distal boss and ventro-median process; hand slender, without process.

Palps (Fig. 15) with basally wide ventral process on proximal femur; other articles unarmed.

Legs 3142, tarsal formula 1-1-3-3.

Penis (Figs 9-14): truncus depressed, bearing needle-like subapical setae in one group on each side. Membraneous socket of glans penis distally round; tube-like stylus more than half as long as truncus, resting in a shallow trench on the dorsal surface of truncus. Basal half of stylus covered by membraneous collar; crescent-shaped apex standing at right angles to axis of stylus.

♀. As the ♂; no external sexual dimorphism discernible.

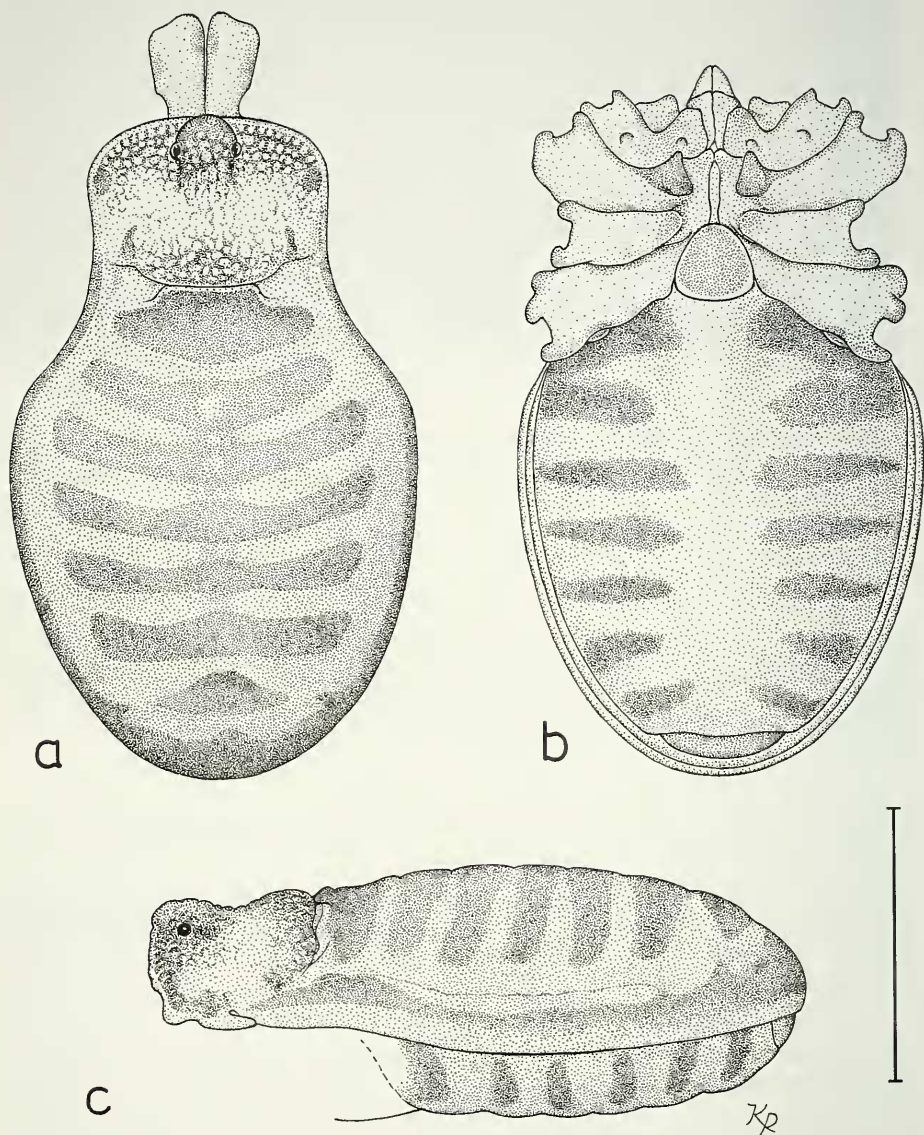


FIG. 17

Caenoncopus tenuis sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Measurements (♂, in brackets ♀): body 2.32 (2.55) long, 1.50 (1.56) wide; carapace region 0.61 (0.64) long, 0.88 (0.93) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.23 (0.27)	0.38 (0.41)	0.32 (0.34)	0.24 (0.24)	- -	0.41 (0.44)	1.58 (1.70)
Leg I	0.23 (0.23)	0.69 (0.69)	0.43 (0.46)	0.35 (0.36)	0.71 (0.72)	0.06 (0.06)	2.47 (2.52)
Leg II	0.27 (0.31)	0.92 (0.94)	0.56 (0.61)	0.61 (0.61)	1.09 (1.09)	0.06 (0.06)	3.51 (3.62)
Leg III	0.23 (0.23)	0.53 (0.54)	0.43 (0.44)	0.37 (0.37)	0.72 (0.72)	0.06 (0.07)	2.34 (2.37)
Leg IV	0.24 (0.26)	0.85 (0.87)	0.56 (0.55)	0.66 (0.69)	0.98 (1.00)	0.06 (0.07)	3.35 (3.44)

Variation: Measurements of body length/width range: ♂ 2.26-2.52/1.38-1.58 (n = 12); ♀ 2.46-2.55/1.50-1.57 (n = 4). Some ♂♂ (including the holotype) have a smaller ventro-basal process on the palpal femur than shown in Fig. 15. In several ♂♂ the carapace is dorsally less distinctly saddle-shaped than in the holotype (Fig. 17c).

Bionomics: The specimens were collected by sifting leaf litter and soil in abandoned rubber and coffee plantations (SE of Payakumbuh) and in a steeply sloping secondary forest (Palopo Nature Reserve).

***Caenoncopus affinis* sp. n.**

Figs 18-26

Material: SUMATRA, West Sumatra Province, Panti, 250 m, ♂ holotype (MHNG), 2 ♂, 2 ♀ paratypes (MAR, MHNG), 19.XI.1989; all leg. D. Agosti, I. Löbl & D. Burckhardt. - Road from Lubuksikaping to Panti, ca. 700 m, 26.X.1991, 1 ♀ paratype, leg. A. Riedel (MAR).

Etymology: Latin: *affinis* = related, neighbouring. The species name points to a close relationship with *C. tenuis* sp. n.

Diagnosis: Very close to *C. tenuis* sp. n. but distinguished by posterior carapace low; genital operculum with straight lateral margins; dark lateral patches on ventral scutum larger, interconnected posteriorly; ventral processes on palpal trochanter and femur more pronounced. Membraneous socket of glans penis more pointed distally; stylus shorter, less strongly sigmoid distally, apex different in shape (Figs 18-23).

Description: ♂ (holotype). Coloration: Body mostly light amber, except dark reticulation on carapace, dark margin and transverse bands on abdominal part of dorsal scutum (Fig. 26a); lateral pairs of dark transverse patches on ventral scutum interconnected posteriorly (Fig. 26b). Genital operculum, process on coxae II, tibia II, proximal 2/3 of metatarsus II and proximal 1/2 of metatarsus I darkened.

Carapace short, interocular area elevated above rest of carapace; abdominal parts of dorsal and ventral scuta smooth, without furrows or elevations (Figs 26a, c). Ventral prosoma with distinct conical process on proximal coxa II, smaller knob-shaped processes on sub-proximal and median coxa I and on palpal coxa. Genital operculum with straight lateral margins, almost trapezoidal in shape (Fig. 26b).

Chelicerae (Fig. 25) small; proximal article with dorso-distal boss and low ventro-median process; hand slender.

Palps (Fig. 24) with distinct ventral process on proximal femur and on distal trochanter.

Legs 3142, tarsal formula 1-1-3-3.

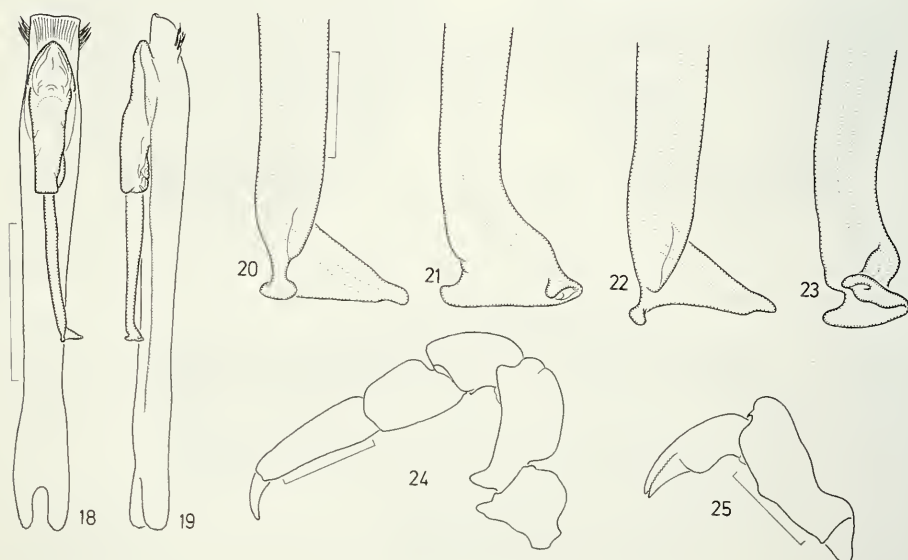
Penis (Figs 18-23): truncus depressed with straight distal margin, bearing a subapical group of needle-like setae on each side. Membranous socket of glans distally tapering; tube-like stylus less than half as long as truncus, slightly bent below apex, basal half covered by membranous collar; apex of stylus crescent-shaped, perpendicular to axis.

♀. As the ♂: no external sexual dimorphism discernible.

Measurements (♂, in brackets ♀): body 3.04 (3.20) long, 1.94 (2.06) wide; carapace region 0.75 (0.75) long, 1.14 (1.14) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.37 (0.38)	0.53 (0.52)	0.44 (0.43)	0.35 (0.34)	- -	0.55 (0.56)	2.24 (2.23)
Leg I	0.29 (0.31)	0.87 (0.81)	0.60 (0.58)	0.47 (0.46)	0.92 (0.90)	0.05 (0.06)	3.20 (3.12)
Leg II	0.34 (0.38)	1.16 (1.08)	0.75 (0.72)	0.78 (0.75)	1.40 (1.31)	0.08 (0.11)	4.51 (4.35)
Leg III	0.31 (0.29)	0.69 (0.66)	0.59 (0.58)	0.47 (0.47)	0.99 (0.95)	0.06 (0.08)	3.11 (3.03)
Leg IV	0.34 (0.39)	1.07 (1.01)	0.78 (0.76)	0.85 (0.82)	1.34 (1.28)	0.06 (0.08)	4.44 (4.34)

Variation: Measurements of body length/width range: ♂ 3.04-3.25/1.90-2.00 (n = 3); ♀ 3.20-3.24/1.96-2.12 (n = 3). One ♂ paratype with interocular tubercle lower than in Fig. 26c.



FIGS 18-25

Caenoncopus affinis sp. n.: ♂ holotype (18-21), ♂ paratype (22-23), ♀ paratype (22-25). - Penis, dorsal (18) and lateral view (19); apex of stylus, dorsal (20, 22) and lateral view (21, 23); left palp, retrolateral view (24); left chelicera, retrolateral view (25). - Scale lines 0.05 mm (20-23), 0.5 mm (18-19, 24-25).

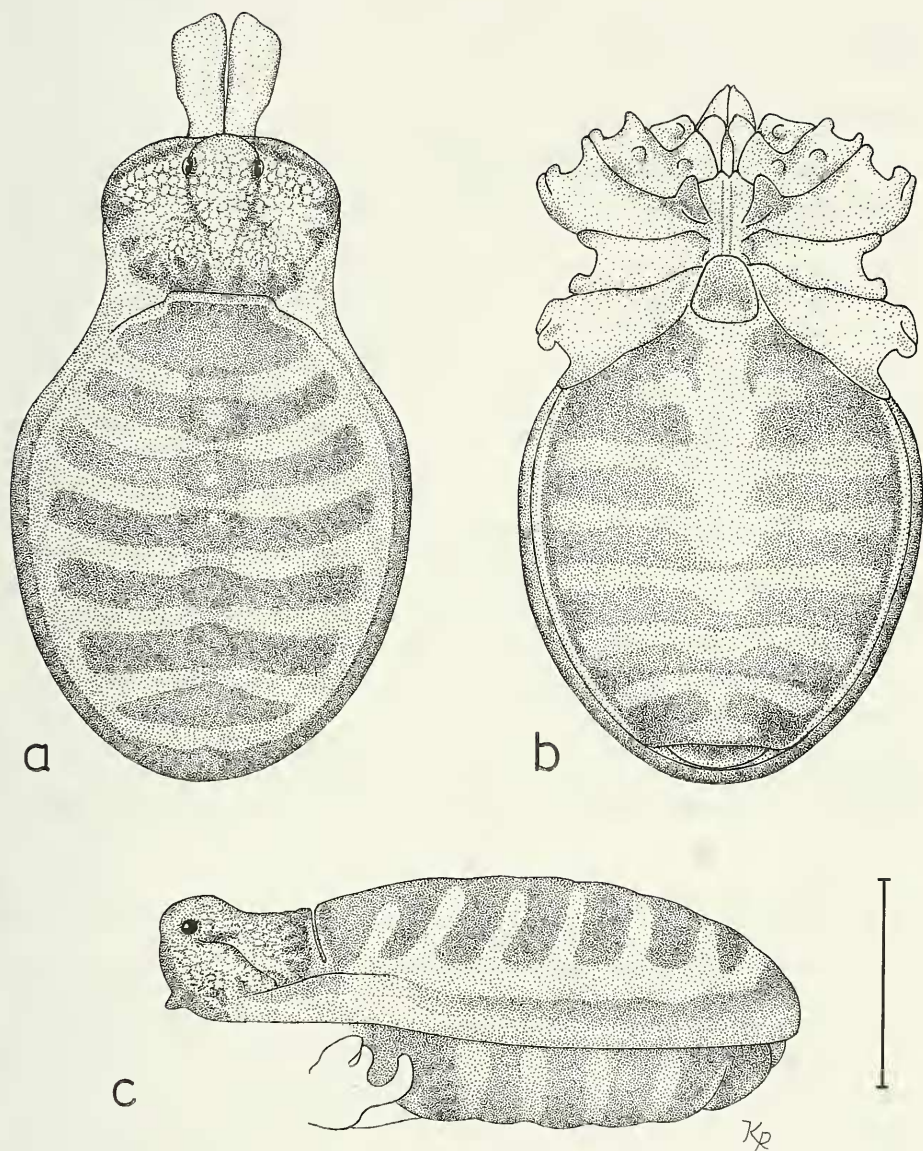


FIG. 26

Caenoncopus affinis sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Bionomics: The specimens were collected by sifting vegetational debris in a lowland swamp forest (near Panti) and in a lowland rain forest (between Lubuksikaping and Panti).

Palaeoncopus gen. n.

Diagnosis: Truncus penis very slender, cylindrical, basally truncate and sub-basally constricted; short subapical glans distad-directed, composed of a short thin stylus surrounded by a pair of forceps-like lateral sclerites interconnected by a median plate; pair of membraneous tubes absent; glans not expandable. Body small; interocular area a round hump, abruptly separated from thoracic area carrying a pair of humps. Anterior margin of abdominal part of dorsal scutum with a pair of wide lobes, more or less distinctly separated from carapace hind-margin by a membraneous zone. Scutal areas distinctly elevated, medially subdivided by a deep longitudinal furrow. Chelicerae small, weak, without modifications apart from dorso-distal hump on proximal article. Palpal femur with a distinct ventro-basal process; palpal trochanter with a large, multilobate ventral process and a conical prodorsal process. Legs 1324, tarsal formula 1-1-3-3. External sexual dimorphism unknown.

Etymology: Greek: *palaios* = old; *oucos* = swelling; *podos* = foot; male gender. The Latinized name (correctly spelled "Palaeoncopus", one "o" omitted) refers to the primitive genital morphology of this genus and to its relationship with *Oncopus*.

Type species: *Palaeoncopus gunung* sp. n.

Species account and distribution: Including three species from Sumatra, i.e. *P. gunung* sp. n., *P. kerdil* sp. n., *P. katik* sp. n.

Relationships: *Palaeoncopus* gen. n. represents the most basic group within the Oncopodidae. The three species are closely related to each other and are known from distinctly separated localities. Presently, they are all to be considered morpho-species.

Palaeoncopus gunung sp. n.

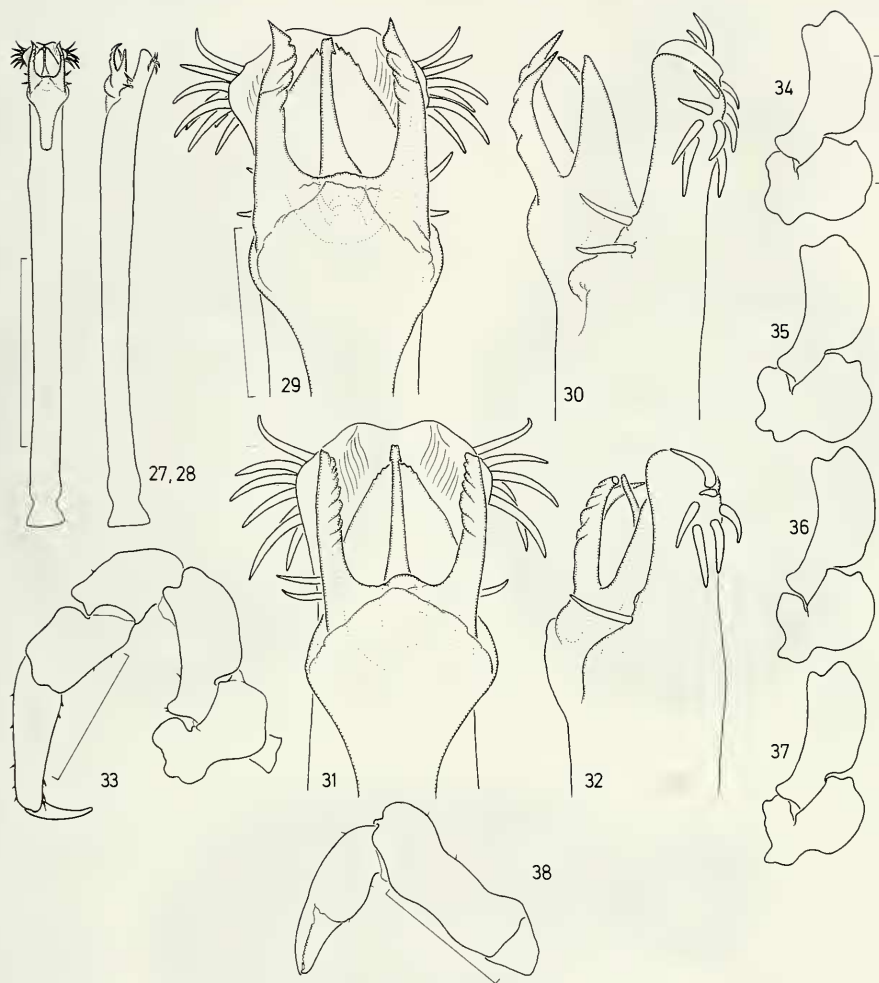
Figs 4a, 27-39

Material: SUMATRA, West Sumatra Province, Bukittinggi, Mt. Singgalang, 2100-2600 m, ♂ holotype (MHNG), 1 ♂, 4 ♀ paratypes (MAR, MHNG); 16.X.1990, leg. A. Riedel.

Etymology: Malay and Indonesian: *gunung* (*gunong*) = mountain. Noun in apposition.

Diagnosis: Resembling *Caenoncopus affinis* sp. n. in body size, proportions and tarsal formula but thoracic area and scutal areas distinctly elevated and subdivided by a deep median furrow; no ventral process on proximal article of chelicera; palpal trochanter with a large, trilobed ventral process and a conical prodorsal process; antero-proximal process on ventral coxa III present; legs 1324. Penis with short distad-directed glans bearing forceps-like lateral sclerites connected by a median plate (Figs 27-32).

Description: ♂ (holotype). Coloration: Body mostly light amber; dark reticulations on carapace and dark, medially broken transversal bands on dorsal (Fig. 39a) and ventral scutal areas (Fig. 39b), indistinct in ventral areas III-V. Limbs mostly dark



FIGS 27-38

Palaeoncopus gunung sp. n.; ♂ holotype (27-30, 34), ♂ paratype (31-32, 35), ♀ paratypes (33, 36-38). - Penis, dorsal (27) and lateral view (28); apex of penis, dorsal (29, 31) and lateral view (30, 32), glans slightly expanded (29-30); left palp, retrolateral view (33); left palp, trochanter and femur, retrolateral view (34-37); left chelicera, retrolateral view (38). - Scale lines 0.5 mm (27-28, 33-38), 0.1 mm (29-32).

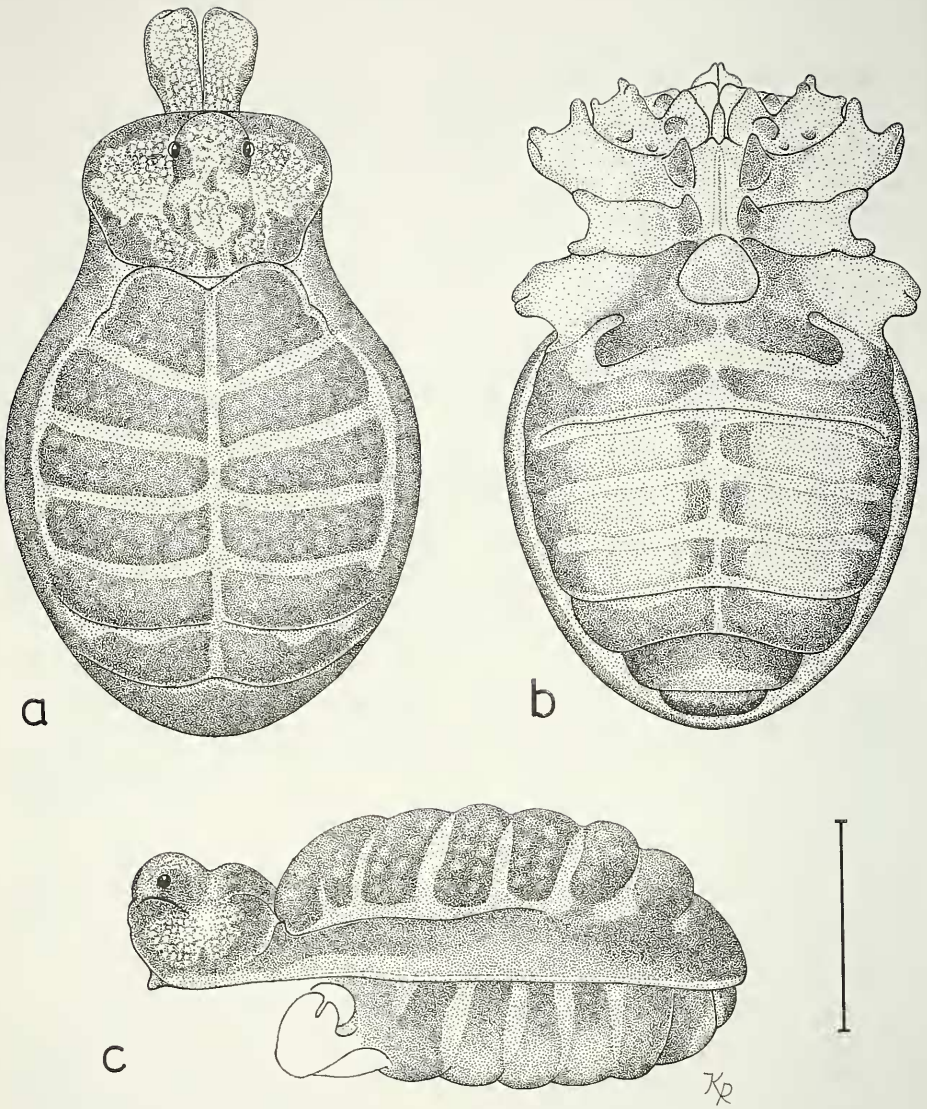


FIG. 39

Palaeoncopus gumung sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

brown, except for light orange cheliceral hand and tarsi, distal tibiae and metatarsi of legs and pedipalps.

Carapace short, narrow depression separating hump on interocular area from pair of humps on thoracic area; dorsal and ventral scutal areas distinctly elevated, dorsal areas separated from each other by deep transverse furrows and by a longitudinal median furrow (Figs 39a, c). Conical antero-proximal processes on ventral coxae II and III, knob-shaped central ones on median coxa I and palpal coxa. Genital operculum wide, subtriangular (Fig. 39b).

Chelicerae (Fig. 38) small; proximal article with dorso-distal boss but without ventro-median process; hand slender.

Palps (Fig. 33-37): femur with conical ventral process; trochanter with large trilobate ventral process and small conical dorsal process.

Legs 1324, tarsal formula 1-1-3-3.

Penis (Figs 27-32): truncus slender, its distal margin arched and medially invaginated, forming two distinct lobes; strong, curved subapical setae in two distinctly separated groups on each side of truncus. Glans pointing distad, rising from a long, basally narrow membranous socket; lateral sclerites tapering, with furrows on lower face. Median plate long, triangular; stylus slender.

♀. As the ♂; no external sexual dimorphism discernible.

Measurements (♂, in brackets ♀): body 2.87 (2.94) long, 1.90 (1.99) wide; carapace region 0.75 (0.69) long, 1.11 (1.10) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.34 (0.32)	0.46 (0.42)	0.42 (0.40)	0.29 (0.26)	- -	0.53 (0.50)	2.04 (1.90)
Leg I	0.31 (0.29)	0.75 (0.75)	0.49 (0.50)	0.46 (0.46)	0.85 (0.85)	0.08 (0.08)	2.94 (2.93)
Leg II	0.38 (0.34)	1.05 (1.04)	0.63 (0.64)	0.76 (0.75)	1.30 (1.28)	0.12 (0.11)	4.24 (4.16)
Leg III	0.29 (0.29)	0.70 (0.67)	0.50 (0.53)	0.50 (0.49)	0.99 (0.98)	0.09 (0.08)	3.07 (3.04)
Leg IV	0.32 (0.31)	0.98 (0.95)	0.67 (0.69)	0.82 (0.79)	1.39 (1.36)	0.11 (0.09)	4.29 (4.19)

Variation: Measurements of body length/width range: ♂ 2.87/1.79-1.90 (n = 2); ♀ 2.94-2.97/1.94-2.03 (n = 4). Variation in the shape of the ventral process on palpal trochanter (Figs 33-37) does not show sexual dimorphism.

Bionomics: The specimens were sifted from leaf litter in a montane forest.

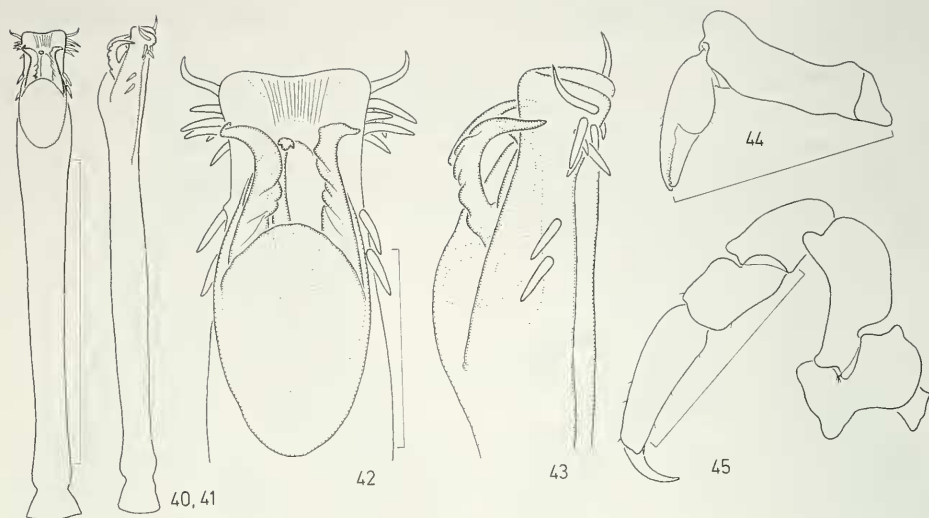
Palaeoncopus kerdil sp. n.

Figs 40-46

Material: SUMATRA, Aceh Province, Mt. Leuser National Park, Ketambe Research Station, 300-500 m, 23.-30.XI.1989, ♂ holotype and ♀ paratype; leg. D. Agosti, I. Löbl & D. Burckhardt (MHNG).

Etymology: Malay and Indonesian: *kerdil* = small, dwarfish.

Diagnosis: Close to *P. gunung* sp. n., distinguished by smaller body size; thoracic area of carapace more elevated; wider gap between carapace and abdominal part of dorsal scutum; dark pattern on ventral scutum different; ventral process on palpal trochanter bilobed. Penis with narrower, truncate apex; short glans more remote from apex; lateral sclerites more strongly bent and closer to each other; membranous socket at base of glans shorter, ovoid (Figs 40-43).



FIGS 40-45

Palaeoncopus kerdil sp. n.; ♂ holotype (40-43), ♀ paratype (44-45). - Penis, dorsal (40) and lateral view (41); apex of penis, dorsal (42) and lateral view (43); left chelicera, retrolateral view (44); left palp, retrolateral view (45). - Scale lines 0.5 mm (40-41, 44-45), 0.1 mm (42-43).

Description: ♂ (holotype). Coloration: Body light amber; dark reticulations on carapace, abdominal part of dorsal scutum with dark margin and medially broken transversal bands on elevated areas (Fig. 46a); dark transverse bands on ventral scutal areas medially indistinct, not broken (Fig. 46b). Proximal leg articles slightly darkened; pedipalps, chelicerae and distal leg metatarsi and tarsi light orange.

Carapace short, hump-shaped interocular area low, separated from thoracic area (with pair of humps) by a narrow depression; dorsal scutal areas distinctly elevated (Fig. 46c), separated from each other and medially by deep furrows (Fig. 46a, c). Ventral scutum with indistinctly elevated areas and lobes behind spiracles. Ventral coxae II and III with distinct antero-proximal processes, coxa II also with postero-proximal one, smaller knob-shaped processes on central coxa I and palpal coxa. Genital operculum widely subtriangular (Fig. 46b).

Chelicerae (Fig. 44) small; proximal article with moderately wide dorso-distal boss, ventral process indistinct; hand slender.

Palps (Fig. 45): femur with conical ventrobasal process; trochanter with large bilobed ventral and small conical dorsal process.

Legs 1324, tarsal formula 1-1-3-3.

Penis (Figs 40-43): truncus slender, apex narrow, distal margin slightly indented; subapical setae in two widely separated groups on each side. Glans short,

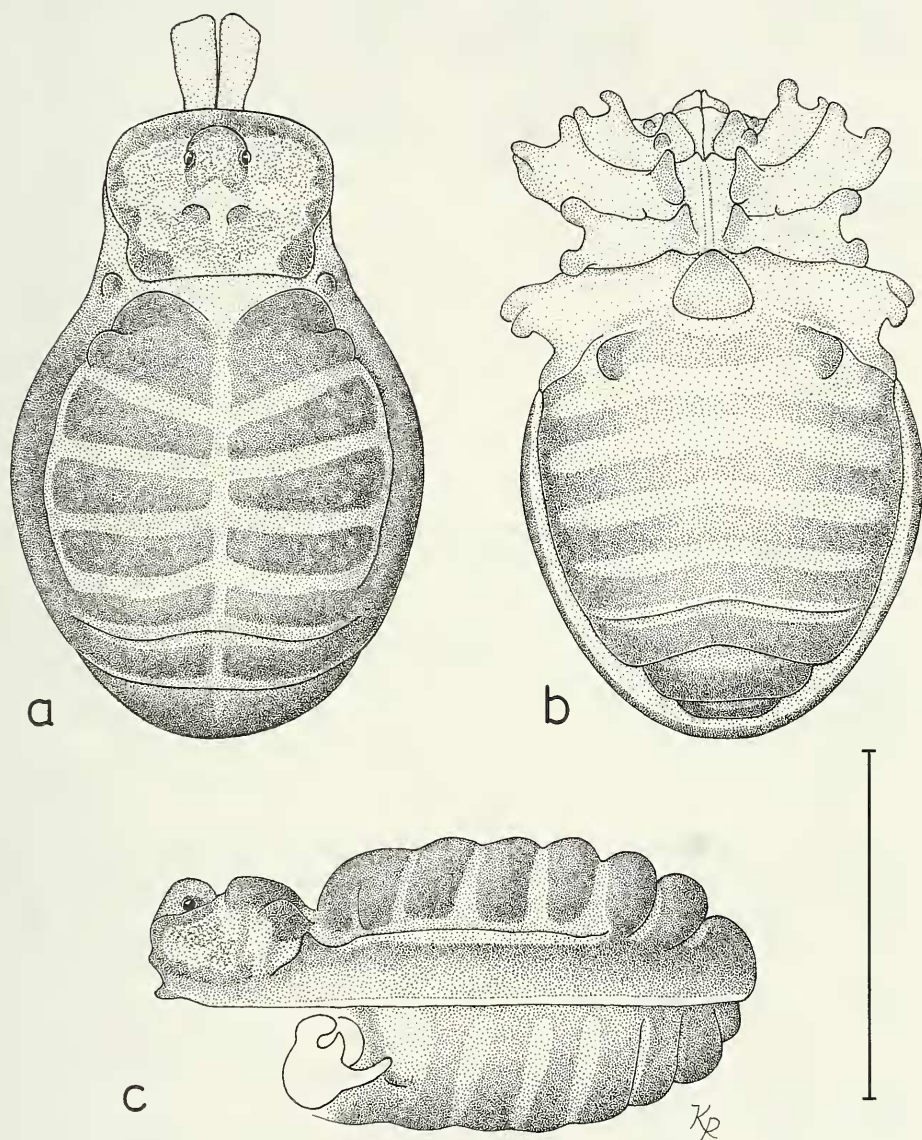


FIG. 46

Palaeoncopus kerdil sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

not reaching apex of penis, rising from a fairly short, ovoid membraneous socket; lateral sclerites distinctly bent, tapering, with furrows on lower face; median plate rounded, its lateral margins hidden under lateral sclerites; stylus slender.

♀. As the ♂; no external sexual dimorphism evident.

Measurements (♂, in brackets ♀): body 1.72 (1.88) long, 1.12 (1.19) wide; carapace region 0.46 (0.47) long, 0.63 (0.71) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.18 (0.21)	0.24 (0.24)	0.24 (0.24)	0.14 (0.14)	- -	0.31 (0.32)	1.11 (1.15)
Leg I	0.16 (0.17)	0.44 (0.46)	0.29 (0.33)	0.24 (0.24)	0.46 (0.50)	0.06 (0.07)	1.65 (1.77)
Leg II	0.20 (0.21)	0.63 (0.64)	0.40 (0.41)	0.37 (0.38)	0.78 (0.77)	0.08 (0.08)	2.46 (2.49)
Leg III	0.17 (0.18)	0.39 (0.40)	0.32 (0.34)	0.26 (0.27)	0.56 (0.56)	0.05 (0.07)	1.75 (1.82)
Leg IV	0.20 (0.20)	0.56 (0.58)	0.43 (0.43)	0.43 (0.46)	0.81 (0.82)	0.07 (0.07)	2.50 (2.56)

Bionomics: The animals were collected by sifting leaf litter in a lowland dipterocarp forest.

***Palaeoncopus katik* sp. n.**

Figs 47-57

Material: SUMATRA, North Sumatra Province, Langkat, Bukit Lawang Nature Reserve, Bohorok River, 5.VII.1984. ♂ holotype and ♂ paratype; leg. J. Robert (MHNG).

Etymology: Malay and Indonesian: *katik* = small, stunted.

Diagnosis: Very similar to *P. kerdil* sp. n. but larger, eye tubercle (in dorsal view) closer to anterior carapace margin, anterior borders of abdominal part of dorsal scutum less arched, legs 1342. Apex of truncus penis arched, bearing two indistinctly separated groups of subapical setae on each side; membraneous socket of glans constricted proximally, lateral sclerites of glans distally wider (Figs 47-52).

Description: ♂ (holotype). Body coloration as in *P. kerdil* sp. n. except for darker palpal femora.

Carapace with domed interocular area close to anterior margin, separated from pair of humps on thoracic area by a narrow depression; wide membraneous zone between carapace and abdominal part of dorsal scutum (Figs 55-57); dorsal scutal areas elevated, separated by deep furrows; ventral scutal areas moderately elevated. Processes on ventral coxae I, II, III and palps. Genital operculum wide; area behind spiracles drawn into lobes.

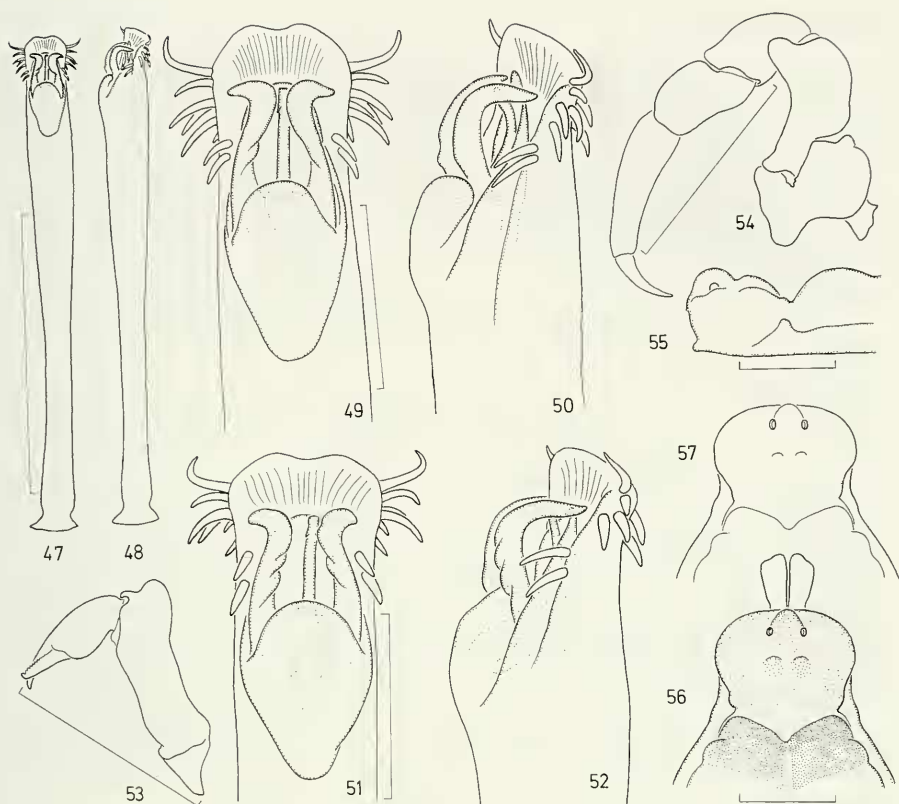
Chelicerae (Fig. 53) small, with dorso-distal boss on proximal article.

Palps (Fig. 54) with conical ventrobasal process on femur and large bilobed ventral plus small conical dorsal process on trochanter.

Legs 1342, tarsal formula 1-1-3-3.

Penis (Figs 47-52): truncus slender, apex slightly widened, distal margin medially invaginated, forming two small lobes; subapical setae in two indistinctly separated groups on each side. Glans short; membraneous socket ovoid, proximally narrow; lateral sclerites strongly bent, distally wide, with furrows on lower face; median plate rounded, mostly hidden under lateral sclerites; stylus slender.

♀. Unknown.



FIGS 47-57

Palaeoncopus katik sp. n.: ♂ holotype (47-50, 55-56), ♂ paratype (51-54, 57). - Penis, dorsal (47) and lateral view (48); apex of penis, dorsal (49, 51) and lateral view (50, 52); left chelicera, retrolateral view (53); left palp, retrolateral view (54); anterior part of body, lateral (55) and dorsal view (56-57). - Scale lines 0.5 mm (47-48, 53-57), 0.1 mm (49-52).

Measurements (♂): body 1.85 long, 1.24 wide; carapace 0.50 long, 0.72 wide.

- Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.20	0.26	0.25	0.15	-	0.36	1.22
Leg I	0.17	0.50	0.37	0.27	0.59	0.05	1.95
Leg II	0.23	0.75	0.47	0.46	0.92	0.07	2.90
Leg III	0.20	0.44	0.37	0.31	0.64	0.05	2.01
Leg IV	0.21	0.66	0.47	0.52	0.92	0.08	2.86

Variation: The ♂ paratype has body length 1.86, width 1.24.

Relationships: This species is very similar to *P. kerdil* sp. n. Minor but consistent differences in external and genital morphology appear adequate for a species discrimination.

Biantoncopus gen. n.

Diagnosis: Penis with stout cylindrical truncus, basally truncate, subbasally constricted; subapical glans distad-directed, composed of a short thin stylus surrounded by a median plate and a pair of lateral sclerites with apices curved away from the truncus; large pair of membraneous tubes present; parts of glans expandable. Body small, scutal areas low; eye tubercle conical. Chelicerae small, without modifications apart from dorso-distal hump on proximal article. Palpal femur with distinct ventro-basal process; palpal trochanter with large ventral process, without dorsal process. Legs 1324, tarsal formula 2-2-3-3. External sexual dimorphism unknown.

Etymology: The genus name refers to similarities in penis morphology with the genus *Biantes* (Biantidae).

Type species: *Biantoncopus fuscus* sp. n.

Species account and distribution: At present the genus includes only the type species from Leyte Island, Philippines.

Relationships: *Biantoncopus* gen. n. distinctly stands apart from the other genera of Oncopodidae, but its relationships are not clear. Penis morphology is similar to that of *Palaeoncopus* gen. n., both genera possess a distad-directed glans. However, glans direction is the only diagnostic character shared with *Palaeoncopus* species and according to the interpretation given in this paper, it presents a symplesiomorphy. Additional genital characters (i.e. expandable glans with a pair of membraneous tubes: mt in Figs 62, 64-65 and 134c) actually show *B. fuscus* sp. n. to be quite different from *Palaeoncopus* gen. spp. n. In the expanded state the tip of the stylus far surmounts the tip of the truncus and both inflated membraneous tubes are bent downwards, pointing to the base of the truncus (Figs 64-65). Morphological and operational similarities to the penes of *Biantes* spp. (Biantidae; MARTENS 1978) are considerable.

On the other hand the habitus of *B. fuscus* sp. n. generally corresponds well with *Gnomulus* species and they also share the tarsal formula 2-2-3-3. Therefore *Biantoncopus* gen. n. may also be interpreted as a *Gnomulus* with reversal in glans orientation or as a separate lineage with partly conservative and partly derived penis morphology (see Fig. 134). Additional related species are expected to be discovered in the future, which hopefully will elucidate the role this glans type plays in oncopodid evolution.

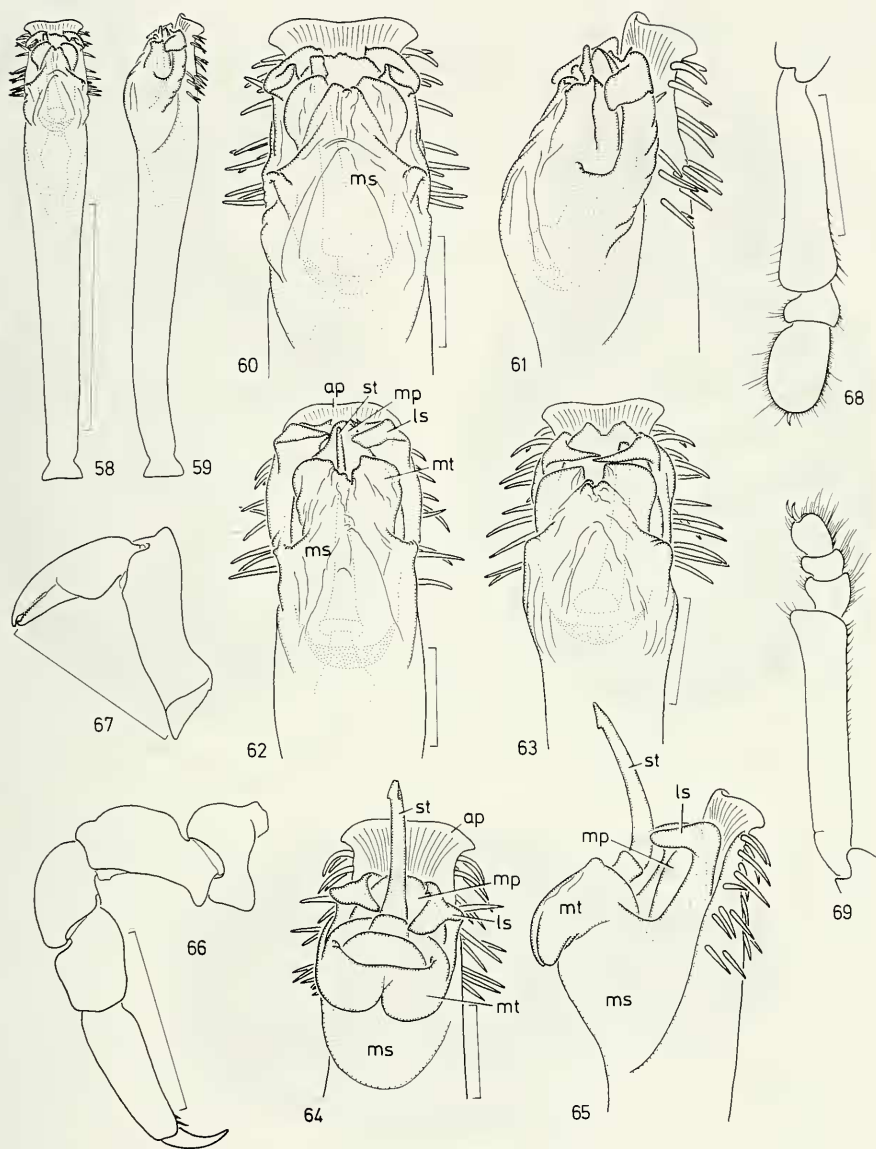
***Biantoncopus fuscus* sp. n.**

Figs 58-70

Material: PHILIPPINES, Leyte, Lake Danao, 500 m, ♂ holotype (MHNG), 2 ♂, 4 ♀ paratypes (MAR, MHNG), 19.II.-9.III.1991, leg. W. Schawaller & J. Martens. - Visca, N of Baybay, 200-500 m, 1 ♂ paratype (MAR), 2.III.1991, leg. W. Schawaller & J. Martens.

Etymology: Latin: *fuscus* = brown; the species name refers to the distinct brownish colour of the body.

Diagnosis: Externally similar to *Gnomulus maculatus* sp. n., but colour pattern different, palpal processes larger and genital operculum wider. Penis stout, glans with distad-directed expandable pair of membraneous tubes and a protrudable stylus (Figs 58-65).



FIGS 58-69

Biantoncopus fuscus n. sp.: ♂ holotype (58-61, 68-69), ♂ paratypes (62-65) [Lake Danao (62, 64-65), N of Baybay (63)], ♀ paratype (66-67). - Penis, dorsal (58) and lateral view (59). Apex of penis, dorsal (60, 62-64) and lateral view (61, 65), glans partly expanded (64-65); left palp, retrolateral view (66); left chelicera, retrolateral view (67); distal part of leg II, retrolateral view (68); distal part of leg IV, prolateral view (69). - Scale lines 0.5 mm (58-59, 66-69), 0.1 mm (60-65).

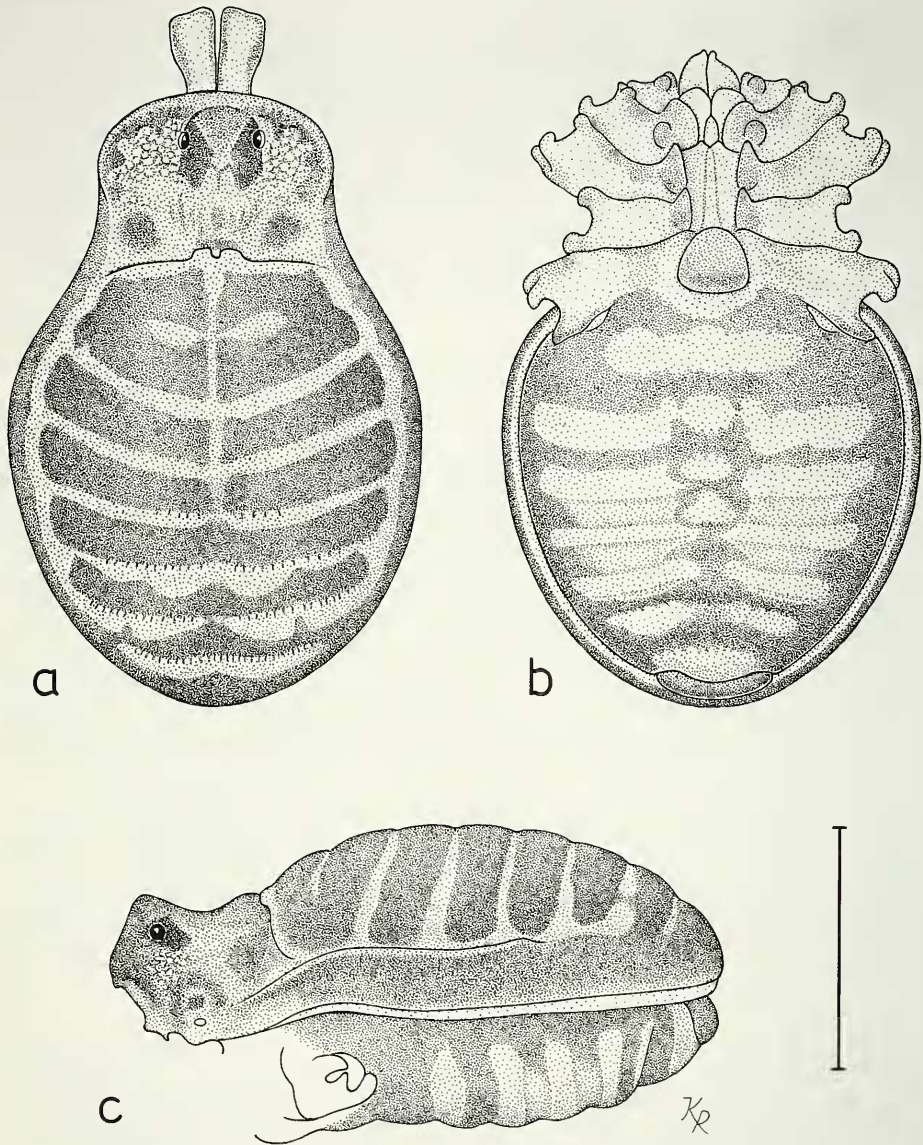


FIG. 70

Biantoncopus fuscus sp. n., ♂ paratype (from the type locality), body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Description: ♂ (paratype). Coloration: Body amber, dark reticulations on: carapace, margin and elevations of scuta, legs (except light orange tarsi) and palps; proximal article of chelicerae dark, chelicerar hand cream; dark transversal bands on dorsal scutal elevations I-IV medially broken (Fig. 70a).

Carapace with conical eye tubercle; a pair of truncate lobes forming bridge between abdominal part of dorsal scutum and carapace (Fig. 70a, c); dorsal and ventral scutal areas only slightly elevated (Figs 70c). Ventral coxae II and III with conical anterio-proximal processes, ventral coxae I and palpal coxae with knob-shaped central processes; genital operculum wide, broadly rounded when closed (Fig. 70b), a pointed anterior process visible when opened.

Chelicerae (Fig. 67) weak; proximal article with a conical dorso-distal process, no ventral one; hand slender.

Palps (Fig. 66): ventral femur with distinct conical proximal process; trochanter with large bilobed ventral process, no dorsal process.

Legs (Figs 68-69) 1324, tarsal formula 2-2-3-3.

Penis (Figs 58-65): truncus stout, its distal margin more or less distinctly invaginated medially; subapical setae in one large group on each side. Glans short, not reaching apex, membranous socket not sharply outlined from truncus; wide lateral sclerites bent dorsad (pointing away from apex), embracing median plate, short, slender stylus and large pair of membranous tubes (corresponding to titillatores in Biantidae; MARTENS 1978). Expanded glans with membranous tubes folded downwards and stylus stretching forward, extending far beyond apex of penis (Figs 64-65).

♀. As the ♂; no external sexual dimorphism discernible.

Measurements (♂, in brackets ♀): body 2.48 (2.60) long, 1.69 (1.73) wide; carapace region 0.64 (0.64) long, 0.93 (0.92) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.23 (0.23)	0.34 (0.32)	0.32 (0.32)	0.21 (0.18)	- -	0.43 (0.43)	1.53 (1.48)
Leg I	0.23 (0.23)	0.59 (0.56)	0.40 (0.37)	0.32 (0.32)	0.50 (0.49)	0.37 (0.35)	2.41 (2.32)
Leg II	0.27 (0.27)	0.76 (0.71)	0.47 (0.46)	0.44 (0.44)	0.76 (0.73)	0.43 (0.41)	3.13 (3.02)
Leg III	0.24 (0.24)	0.52 (0.50)	0.40 (0.38)	0.34 (0.34)	0.65 (0.64)	0.28 (0.25)	2.43 (2.35)
Leg IV	0.29 (0.26)	0.72 (0.69)	0.50 (0.49)	0.53 (0.53)	0.93 (0.92)	0.32 (0.31)	3.29 (3.20)

Variation: Body length/width ranges: ♂ 2.25-2.48/1.60-1.69 (n = 4), ♀ 2.37-2.60/1.59-1.73 (n = 4). Bridge teeth connecting abdominal part of dorsal scutum and carapace vary in shape from indistinct and rectangular to distinct and triangular or rounded. One ♂ (from the type locality) has a thin cylindrical stylus and a narrowly rounded median plate with a smooth margin (Fig. 62). In all other ♂♂ the stylus is fairly broad and slightly depressed and the median plate is broadly rounded with a more or less strongly indented anterior margin (Figs 60-61, 63-65).

Bionomics: The specimens were extracted from soil and leaf litter on plane and strongly sloping forest floor of a primary evergreen forest interspersed by clearings with cultivated bananas.

Gnomulus Thorell, 1890

Gnomulus Thorell (1890: 378), type species originally designated but described later, *G. sumatranus* Thorell, 1891; Pocock (1897: 285); Roewer (1923: 60-61); Schwendinger (1992: 197).

Pelitus Thorell (1891: 757), type species by original designation, *P. armillatus* Thorell, 1891; Pocock (1897: 285); Roewer (1923: 62); Sørensen (1932: 213); Schwendinger (1992: 197). NEW SYNONYMY.

Diagnosis (extended): Penis with basally truncate, subbasally constricted cylindrical truncus. Subapical glans proximad-directed, stylus flanked by a pair of sclerites (both structures variable in shape and length) and a pair of membranous tubes; median plate present or absent. Interocular area low or elevated into a domed or conical tubercle. Bridge between carapace and abdominal part of dorsal scutum distinct or absent. Dorsal scutal areas elevated or low, with a more or less distinct longitudinal median furrow. Chelicerae weakly or strongly developed, proximal article with a more or less distinct dorso-distal hump or tubercle, rarely with a ventro-median process; hand unarmed. Palpal femur usually with (rarely without) ventro-basal process, rarely with ventro-median one; palpal trochanter with or without ventral process, dorsal process absent. Legs 1324, 1342, 3124, 3142; tarsal formula 2-2-2-2 or 2-2-3-3. External sexual dimorphism in shape or hair cover of ventral scutal elevations, in shape of carapace or in size of chelicerae.

Species account: Twenty nominal oncopodid species (thirteen previously described and seven new), in which penis morphology is known, are here listed under *Gnomulus*. These are:

G. sumatranus Thorell, 1891 [Sumatra] - Loman 1903: fig. 5f; ♂, ♀ syntypes in MCSNG examined.

G. segnipis (Loman, 1892) **comb. n.**, transferred from *Pelitus* [Sumatra; doubtful records from Java and Borneo] - Schwendinger 1992: figs 58-61 (possibly not conspecific); presumably conspecific ♂♂ from Sumatra in CCD, SMF, ZMA, ZMT examined.

G. aborensis (Roewer, 1913), transferred from *Pelitus* by Roewer (1923: 61-62) [NE-India] - 2 ♂ paratypes in SMF examined.

G. laevis (Roewer, 1915) **comb. n.**, transferred from *Pelitus* [Borneo] - Schwendinger 1992: figs 63-66.

G. insularis (Roewer, 1927) **comb. n.**, transferred from *Pelitus* [Malaysia, Penang Island] - ♂ holotype in SMF examined (probably identical with *G. rostratus* - ♀ holotype in MCSNG examined).

G. drescoi (Šilhavý, 1962) **comb. n.**, transferred from *Pelitus* [Sumatra] - Suzuki 1982: figs 13, 14.

G. inadatei (Suzuki, 1969) **comb. n.**, transferred from *Pelitus* [Brunei] - Suzuki 1969: figs 4a-e.

G. hyatti (Martens, 1977) **comb. n.**, transferred from *Pelitus* [Nepal] - Martens 1977: figs 3, 4.

G. goodnighti (Suzuki, 1977) **comb. n.**, transferred from *Pelitus* [Philippines, Mindanao] - Suzuki 1977: figs 2f-i.

- G. launaiatus* (Schwendinger, 1992) **comb. n.**, transferred from *Pelitus* [Thailand] - SCHWENDINGER 1992: figs 8-13.
- G. baharu* Schwendinger **nom. n.** (Malay and Indonesian: *baharu* = new), homonymously described under *Pelitus thorelli* [Brunei] by SCHWENDINGER 1992: figs 21-26.
- G. couigerus* (Schwendinger, 1992) **comb. n.**, transferred from *Pelitus* [Sabah] - SCHWENDINGER 1992: figs 36-41.
- G. sundaicus* (Schwendinger, 1992) **comb. n.**, transferred from *Pelitus* [Sarawak] - SCHWENDINGER 1992: figs 48-53.
- G. crucifer* sp. n. - Philippines, Luzon.
- G. maculatus* sp. n. - Philippines, Luzon and Mindoro (?).
- G. coniceps* sp. n. - Philippines, Luzon.
- G. leyteensis* sp. n. - Philippines, Leyte.
- G. laruticus* sp. n. - Malaysia, Perak.
- G. asli* sp. n. - Malaysia, Perak.
- G. hirsutus* sp. n. - Malaysia, Selangor and Pahang.

In the remaining eight species described under *Gnomulus* and *Pelitus* penis morphology is yet unknown. Therefore they may belong to either *Gnomulus* or *Biant-oncopus* gen. n., which are indistinguishable by external characters. As *Gnomulus* is by far the more widespread of both genera, we provisionally place these species in *Gnomulus*.

- G. rostratus* Thorell, 1890 [Malaysia, Penang Island] - see *G. insularis* **comb. n.**
- G. armillatus* (Thorell, 1891) **comb. n.**, transferred from *Pelitus* [Sumatra].
- G. annulipes* (Pocock, 1897) **comb. n.**, transferred from *Pelitus* [Sarawak].
- G. pulvillatus* (Pocock, 1903) **comb. n.**, transferred from *Pelitus* [Malaysia, Selangor].
- G. piliger* (Pocock, 1903) **comb. n.**, transferred from *Pelitus* [Malaysia].
- G. thorelli* (Sørensen, 1932) **comb. n.**, transferred from *Pelitus* [Java].
- G. palawaneensis* (Suzuki, 1982) **comb. n.**, transferred from *Pelitus* [Philippines, Palawan].
- G. minor* Tsurusaki, 1990 [Philippines, Luzon].

Distribution: Himalayan Region (Nepal and northeastern India) and Southeast Asia (northern Thailand to Java and the Philippines).

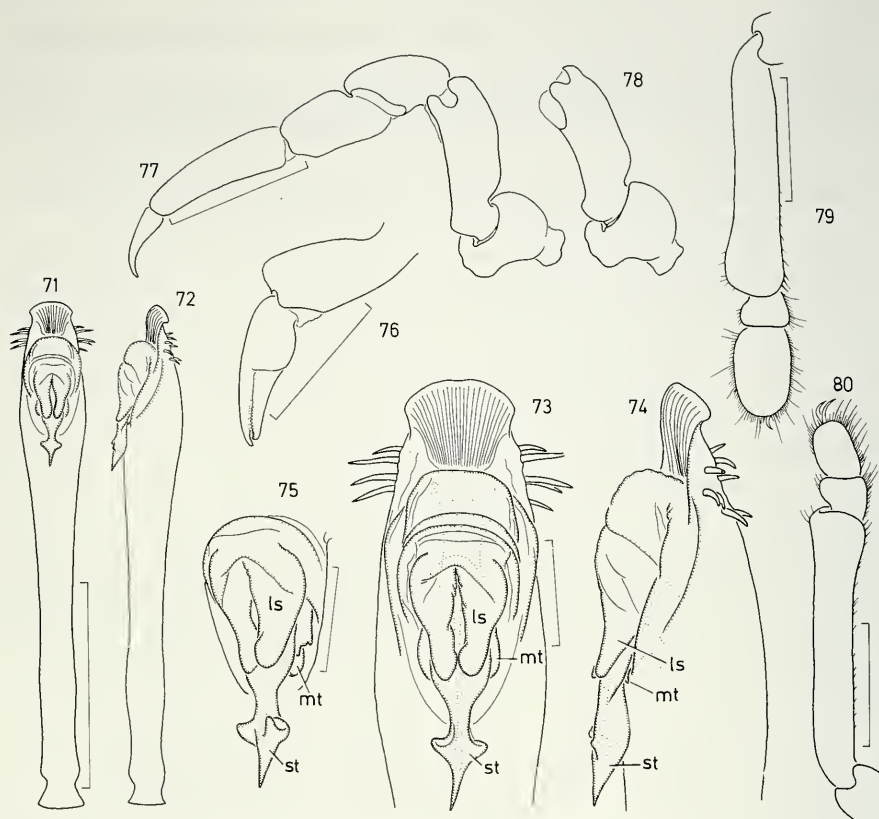
NEW SPECIES OF GNOMULUS

Gnomulus crucifer sp. n.

Figs 71-81

Material: PHILIPPINES, Luzon, Mt. Santo Thomas close to Baguio, ca. 1850 m. ♂ holotype, 14.I.1980; leg. L. Deharveng (MHNG).

Etymology: Latin: *crux* = cross, *ferre* = to carry; the species name refers to the cross-shaped glans penis of this species.



FIGS 71-80

Gnomulus crucifer sp. n., ♂ holotype. - Penis, dorsal (71) and lateral view (72); apex of penis, dorsal (73) and lateral view (74); glans penis, dorso-lateral view (75); left chelicera, retrolateral view (76); left palp, retrolateral view (77); trochanter and femur of left palp, retrolateral view (78); distal part of left leg II, retrolateral view (79); distal part of left leg IV, prolateral view (80). - Scale lines 0.5 mm (71-72, 76-80), 0.1 mm (73-75).

Diagnosis: Similar to *G. minor* Tsurusaki but with elevated interocular area, process on palpal trochanter different in shape, anterio-proximal process on ventral leg coxa II present; legs 1324, tarsal formula 2-2-2-2. Glans penis proximad-directed, bearing an enlarged stylus with cross-shaped apex; lateral sclerites lobate, median plate absent (Figs 71-75).

Description: ♂ (holotype). Coloration: body light amber, with dark reticulations on carapace, dark transversal bands on abdominal part of dorsal scutum and dark, medially broken transverse bands on ventral scutum (Figs 81a, b); genital operculum with indistinct dark reticulation; chelicerae and pedipalps cream, except slightly darker palpal femur; legs grey-brown, except slightly lighter trochanters and cream coxae, tarsi and distal metatarsi.

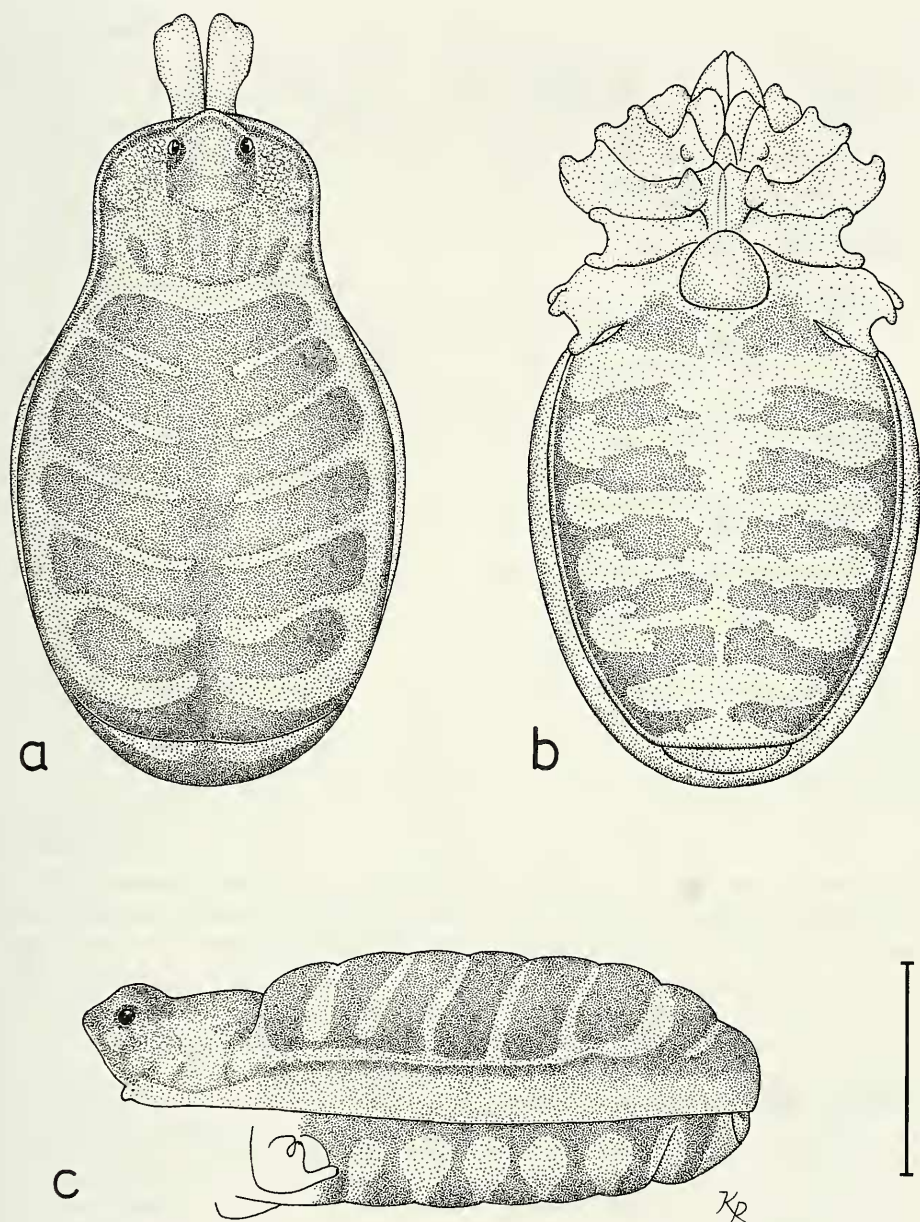


FIG. 81

Gnomulus crucifer sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Carapace with low, broadly rounded eye tubercle (Figs 81a, c); connection between carapace and abdominal part of dorsal scutum indistinct; dorsal and ventral scutal areas only slightly elevated (Fig. 81c). Ventral leg coxae II and III with conical antero-proximal process, coxa II with rounded postero-proximal one; ventral coxae I and palpal coxae with knob-shaped paramedian and small central processes, respectively; genital operculum wide (Fig. 81b).

Chelicerae (Fig. 76) weak; proximal article with dorso-distal boss, no ventral process; hand slender.

Palps (Fig. 77-78): ventral femur with low conical proximal process; trochanter with pronounced, somewhat trilobed ventral process, no dorsal process.

Legs (Figs 79-80) 1324, tarsal formula 2-2-2-2.

Penis (Figs 71-75): truncus fairly slender, apex narrow, with broadly rounded distal margin; subapical setae in one small group on each side. Glans with a long, proximally wide stylus, constricted below a cross-shaped apex with acutely pointed tip; lateral sclerites flat, distally rounded, lying above stylus; median plate absent; pair of membranous tubes partly covered by stylus.

♀. Unknown.

Measurements (♂): body 3.12 long, 1.78 wide; carapace 0.88 long, 1.02 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.31	0.43	0.35	0.26	-	0.49	1.84
Leg I	0.23	0.70	0.41	0.40	0.62	0.43	2.79
Leg II	0.31	0.94	0.50	0.64	1.01	0.49	3.89
Leg III	0.24	0.63	0.44	0.43	0.76	0.30	2.80
Leg IV	0.29	0.93	0.61	0.73	1.11	0.34	4.01

Relationships: Habitus, shape of palps and chelicerae and geographical proximity suggest close relationship with *G. minor* (♂ unknown), although the tarsal formula is different. The penis with an enlarged stylus and without a median plate, on the other hand, distantly resembles that of *Caenoncopus* gen. n. At the present state of knowledge, however, it appears that this partial congruence in penis morphology was caused by parallelism.

Bionomics: The specimen was extracted from vegetational debris in a humid ravine of an evergreen hill forest.

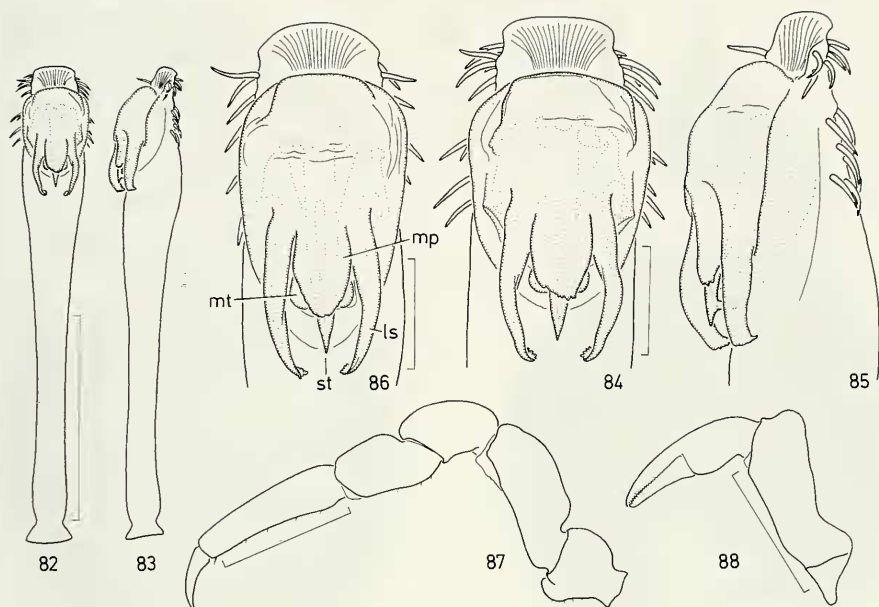
Gnomulus maculatus sp. n.

Figs 82-89

Material: PHILIPPINES, Luzon, Mountain Province, dolines NE of Sagada, ♂ holotype (MHNG), 21.XII.1979; 1 ♂, 1 ♀ paratypes (MAR, MHNG), Sagada, near Latan Cave, 6.I.1980; Sagada, near village and near Sogong Cave, 4., 5., 9.I.1980, 3 juv. (MAR).- Mindoro, Puerto Galera, near San Theodoro Waterfall, 1 ♀ paratype (MAR), 2.-4.I.1979 (probably mislabeled). All specimens leg. L. Deharveng.

Etymology: Latin: *maculatus* = spotted; the species name refers to the conspicuous colour pattern on the dorsal scutum.

Diagnosis: Closely related to *G. goodnighti*, distinguished by distinct colour pattern; eye tubercle lower; dorsal scutum broadly rounded behind, without paramedian humps on posterior scutal areas, with two lobate bridge teeth on anterior



FIGS 82-88

Gnomulus maculatus sp. n.; ♂ holotype (82-85), ♂ paratype (86), ♀ paratype (87-88). - Penis, dorsal (82) and lateral view (83); apex of penis, dorsal (84, 86) and lateral view (85); left palp, retrolateral view (87); left chelicera, retrolateral view (88). - Scale lines 0.5 mm (82-83, 87-88), 0.1 mm (84-86).

margin (none on posterior carapace); small antero-proximal processes present on leg coxae III. Distal margin of truncus penis rounded; membranous socket of glans wide; paired lateral sclerites of glans only little bent, terminally truncate; median plate long, tongue-shaped; stylus stout, with bifurcate apex (Figs 82-85).

Description: ♂ (holotype). Coloration: body light yellow, with dark rings around eyes and dark procurved band on posterior carapace; dorsal scutum very dark along margin and on scutal areas, except for conspicuous light yellow median zone on last 3 scutal areas (Fig. 89a, c); dark transversal bands on ventral scutum unbroken, except for the last one (Fig. 89b); genital operculum grey-yellow, tarsus of leg I cream.

Carapace with conical eye tubercle; lobed bridge teeth between abdominal part of dorsal scutum and carapace; dorsal and ventral scutal areas moderately elevated (Fig. 89a, c). Ventral leg coxae II and III with small antero-proximal processes; ventral coxae I and palpal coxae with knob-shaped median processes; genital operculum wide (Fig. 89b).

Chelicerae (Fig. 88) weak; proximal article with dorso-distal boss, no ventral process; hand slender.

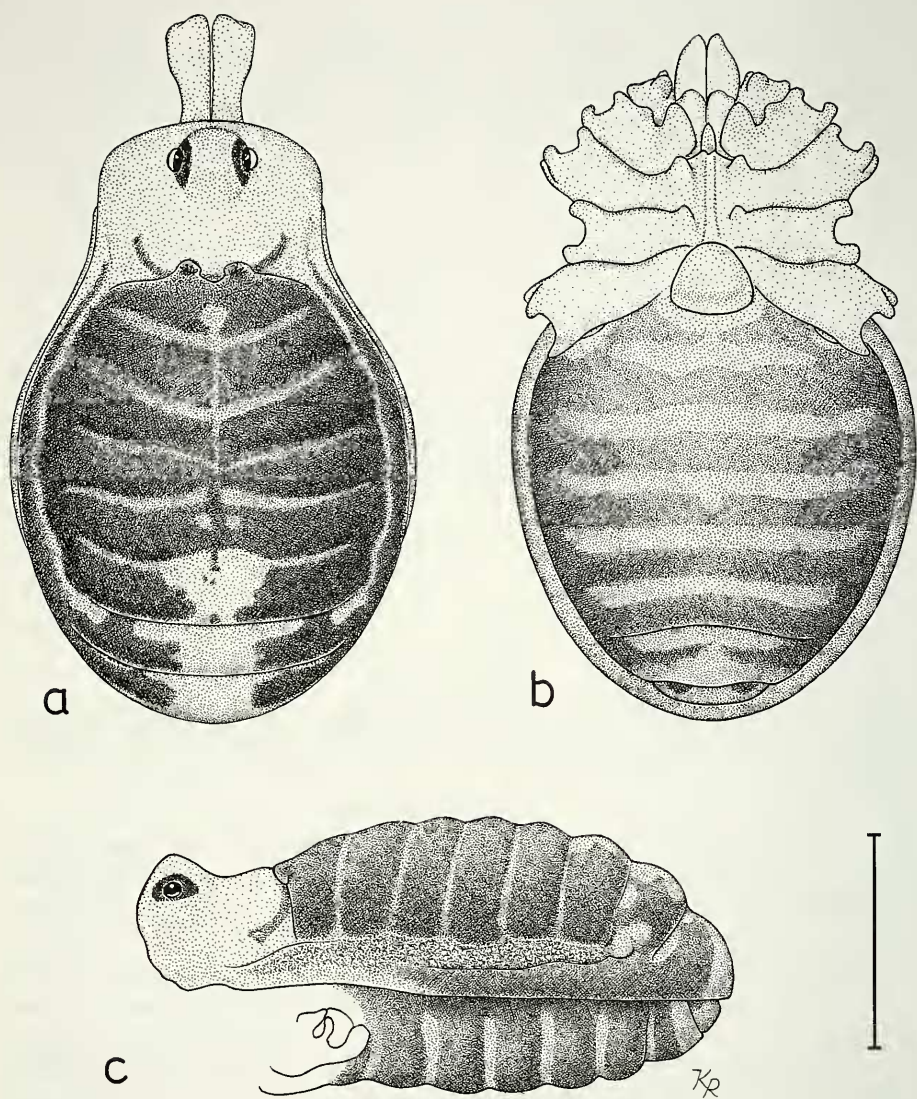


FIG. 89

Gnomulus maculatus sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Palps (Fig. 87): ventral femur with low proximal process; trochanter with distad directed ventral process.

Legs 1324, tarsal formula 2-2-3-3.

Penis (Figs 82-86): truncus fairly slender, apex narrow, distal margin broadly arched, without median indentation; subapical setae in two indistinctly separated groups on each side. Glans rising from a very wide membranous socket; lateral sclerites long, forceps-like, connected by a long, tongue-shaped median plate with finely serrated distal margin; stylus stout, its apex bifurcate, with tip (carrying opening of sperm duct) bending towards the truncus at right angles below a pointed distad directed process; pair of membranous tubes mostly covered by median plate.

♀. As the ♂; no external sexual dimorphism discernible.

Measurements (♂, in brackets ♀): body 2.80 (2.94) long, 1.90 (1.90) wide; carapace region 0.76 (0.69) long, 1.03 (1.04) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.29 (0.29)	0.42 (0.44)	0.35 (0.34)	0.24 (0.24)	- -	0.54 (0.55)	1.84 (1.86)
Leg I	0.24 (0.26)	0.67 (0.69)	0.42 (0.41)	0.43 (0.41)	0.64 (0.66)	0.41 (0.41)	2.81 (2.84)
Leg II	0.34 (0.34)	0.91 (0.90)	0.53 (0.53)	0.63 (0.62)	0.96 (0.99)	0.47 (0.48)	3.84 (3.86)
Leg III	0.27 (0.27)	0.61 (0.63)	0.44 (0.44)	0.46 (0.45)	0.81 (0.80)	0.32 (0.33)	2.91 (2.92)
Leg IV	0.32 (0.32)	0.90 (0.93)	0.59 (0.60)	0.76 (0.75)	1.14 (1.17)	0.35 (0.35)	4.06 (4.12)

Variation: Body length/width ranges: ♂ 2.80-2.84/1.87-1.90 (n = 2), ♀ 2.94-3.18/1.90-2.09 (n = 2). Bridge teeth between abdominal part of dorsal scutum and carapace vary in shape; they are generally smaller in the ♀♀ examined, in one of them missing on the left side. The median plate of the glans penis is narrower in the ♂ paratype (Fig. 86). The largest specimen (♀) is darker than all others, i.e. with dark reticulation on: carapace, genital operculum, leg coxae and trochanters, palps (except tarsus) and proximal chelicerae; femora to metatarsi of legs grey-brown.

Relationships: The enlarged, uniquely formed stylus of this species probably represents an earlier stage of glans modification, which is more strongly developed in *G. crucifer* sp. n. In other characters *G. maculatus* sp. n. most closely resembles *G. goodnighti*.

Bionomics: The specimens were collected from humid leaf litter and moss in an evergreen hill forest by means of sifting and Berlese-extraction.

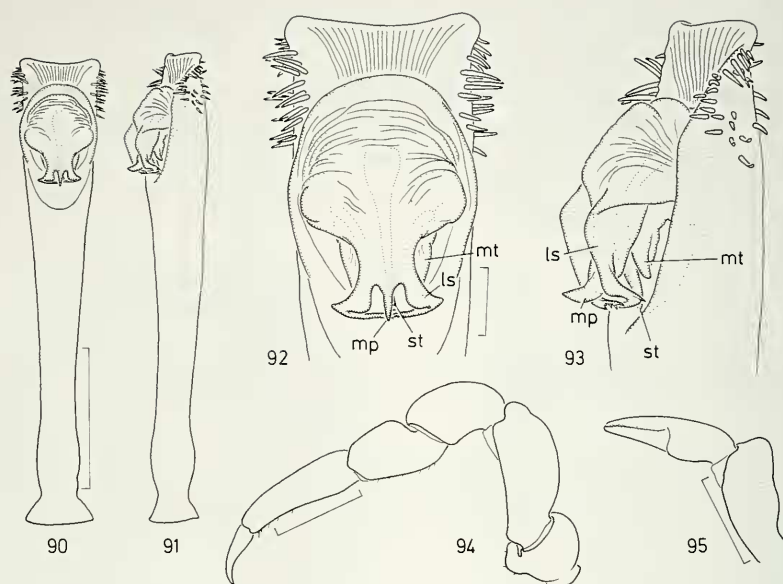
Distribution (Fig. 3): According to the collecting data the specimens are from two Philippine islands, Luzon and Mindoro. This would be an exceptionally wide distribution for an oncopodid species. The record of a single specimen from Mindoro is very probably due to a confusion of labels (supported by L. Deharveng, pers. comm.).

Gnomulus coniceps sp. n.

Figs 90-96

Material: PHILIPPINES, Luzon, Baguio, near Cristal Caves, 1500 m, ♂ holotype (MHNG), 12.I.1980, leg. L. Deharveng.

Etymology: Latin: *conus* = cone; *ceps* (from *caput*) = head; noun in apposition. The name refers to the unusually large eye tubercle of this species.



FIGS 90-95

Gnomulus coniceps sp. n., ♂ holotype. - Penis, dorsal (90) and lateral view (91); apex of penis, dorsal (92) and lateral view (93); left palp, retrolateral view (94); left chelicera, retrolateral view (95). - Scale lines 0.5 mm (90-91, 94-95), 0.1 mm (92-93).

Diagnosis: Closest to *Gnomulus goodnighti*, distinguished by basally wider eye tubercle and narrower genital operculum. Penis with broadly invaginated anterior margin of truncus; glans penis with strongly geniculate lateral sclerites connected to a narrow, pointed median plate (Figs 90-93).

Description: ♂ (holotype). Coloration: body amber, with dark reticulations on carapace (especially around eyes), very dark dorsal scutal areas with a light longitudinal median band between areas II-IV (Fig. 96a); ventral scutal areas with transversal bands becoming increasingly darker posteriorly (Fig. 96b). Chelicerae, pedipalps and legs light amber, except slightly darker metatarsi I-IV and patella and tibia IV; terminal tarsal segment darker than basal ones.

Carapace short, with broadly conical eye tubercle occupying almost entire length of carapace (Fig. 96c); triangular pair of abdominal scutal processes forming bridge with pair of processes from carapace. Abdominal part of dorsal scutum high, with paramedian pairs of humps on scutal areas (largest on V-VII); posterior margin of dorsal scutum slightly pointed (Figs 96a, c); ventral scutum with only slightly elevated areas (Figs 96b, c). Distinct antero- and postero-proximal processes on ventral leg coxa II, a smaller one on coxa III; palpal coxae with large ventral processes; genital operculum longer than wide (Fig. 96b).

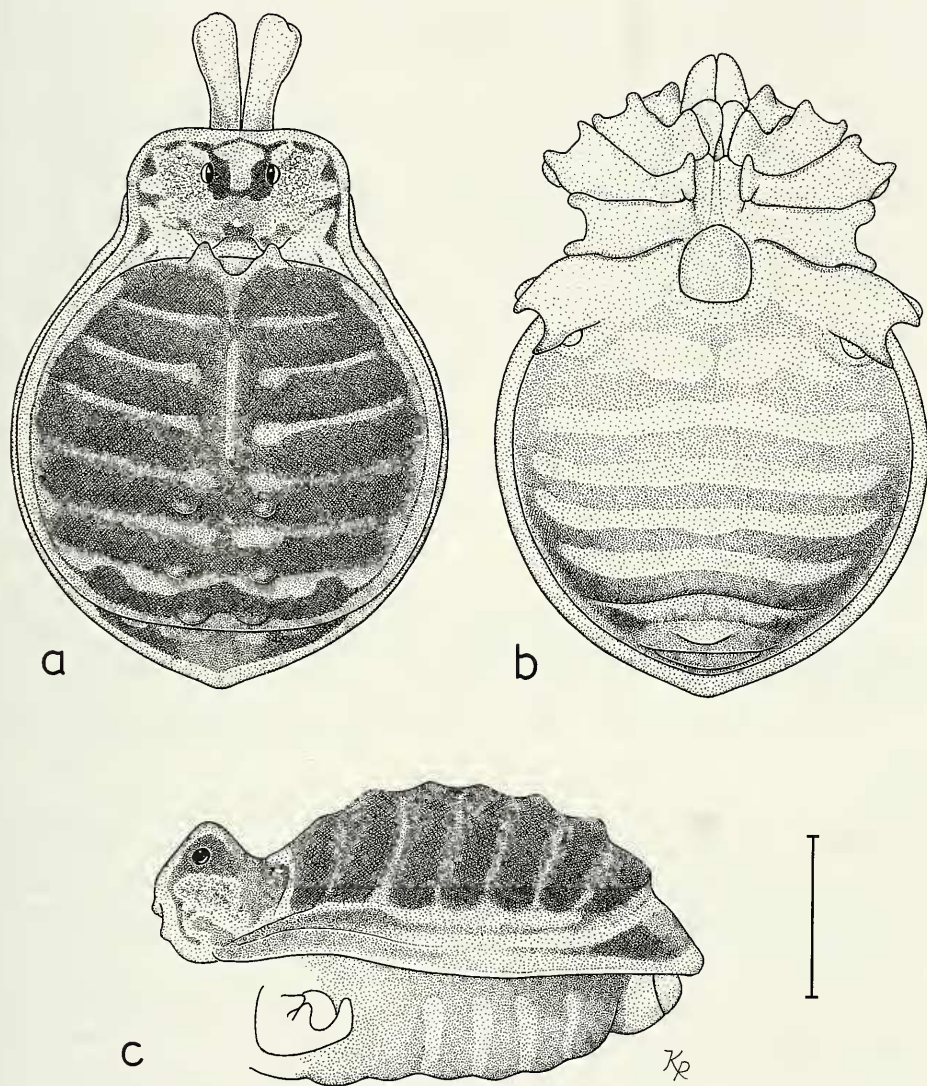


FIG. 96

Gnomulus coniceps sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Chelicerae (Fig. 95) weak; proximal article with dorso-distal boss, no ventral process; hand slender.

Palps (Fig. 94): ventral femur with indistinct proximal process; trochanter with distad-directed ventral process.

Legs 1324, tarsal formula 2-2-3-3.

Penis (Figs 90-93): truncus stout, apex wide, anterior margin broadly invaginated; subapical setae in one large group on each side. Glans medially constricted; lateral sclerites strongly geniculate, proximally divergent, distally convergent, tips ramified, touching each other; lateral sclerites connected by a short, spike-like median plate above slender stylus; pair of membranous tubes clearly visible at constriction of glans.

♀. Unknown.

Measurements (♂): body 3.37 long, 2.66 wide; carapace region 0.78 long, 1.38 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.42	0.61	0.51	0.33	-	0.65	2.52
Leg I	0.33	1.05	0.56	0.64	1.03	0.59	4.20
Leg II	0.35	1.35	0.73	1.02	1.55	0.65	5.65
Leg III	0.32	1.05	0.61	0.76	1.35	0.53	4.62
Leg IV	0.41	1.40	0.73	1.05	1.89	0.61	6.09

Relationships: According to external morphology *G. coniceps* sp. n. is closest to *G. goodnighti* and (more distant) to *G. maculatus* sp. n., but its glans penis is quite different from both of them and shows no close resemblance with any species known so far.

Bionomics: The specimen was collected from a ravine in an evergreen hill forest.

Gnomulus leyteensis sp. n.

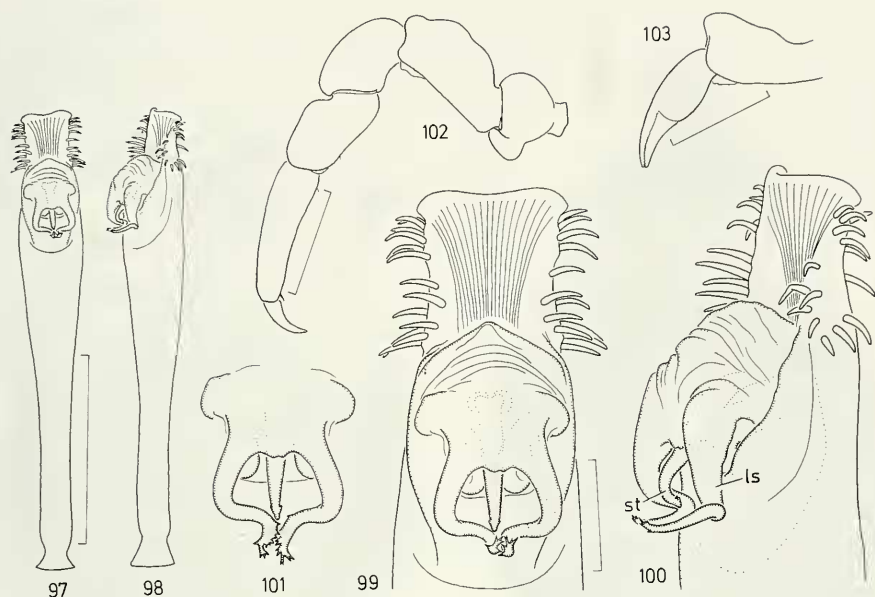
Figs 97-104

Material: PHILIPPINES, Leyte, Visca, north of Baybay, 200-500 m, ♂ holotype (MHNG), 10.III.1991, leg. J. Martens & W. Schawaller.

Etymology: The specific epithet is taken from the name of the island where the species was collected.

Diagnosis: Closest to *G. goodnighti*, distinguished by more rounded posterior margin of body, narrower genital operculum and basally wider ventral process on palpal trochanter. Penis apically narrower; glans more remote from distal margin; lateral sclerites less strongly bent, with ramified tip; median plate indistinct (Figs 97-101).

Description: ♂ (holotype). Coloration: body amber, with dark reticulations on carapace (especially around eyes); dorsal scutum with very dark margin and transversal bands on elevations, in scutal areas I-IV broken by a light longitudinal median band (Fig. 104a); ventral scutal areas with unbroken dark transversal bands (Fig. 104b). Chelicerae, pedipalps and legs light amber, except slightly lighter tarsi and slightly darker metatarsus II.



Figs 97-103

Gnomulus leyteensis sp. n., ♂ holotype. - Penis, dorsal (97) and lateral view (98); apex of penis, dorsal (99) and lateral view (100); glans with tips of lateral sclerites folded downwards (101); left palp, retrolateral view (102); left chelicera, retrolateral view (103). - Scale lines 0.5 mm (97-98, 102-103), 0.1 mm (99-101).

Carapace short, with conical eye tubercle set back from anterior margin; posterior part of carapace flat, triangular pair of paramedian processes forming bridge with corresponding processes on anterior margin of abdominal part of dorsal scutum. Dorsal scutum high, with paramedian pairs of indistinct humps on areas I-VII; posterior margin of dorsal scutum slightly pointed (Figs 104a, c); ventral scutum with only slightly elevated areas (Figs 104b, c). Ventral leg coxa II with distinct anterior- and posterior-proximal processes, coxa III with small anterior-proximal one; palpal coxa with large ventral process; genital operculum about as long as wide (Figs 104b).

Chelicerae (Fig. 103) small, slender; proximal article with dorso-distal boss, no ventral process; hand slender.

Palps (Fig. 102): ventral femur with indistinct proximal process; trochanter with distad-directed, basally wide ventral process.

Legs 1324, tarsal formula 2-2-3-3.

Penis (Figs 97-101): truncus with narrow apex and slightly invaginated distal margin; subapical setae in one large group on each side. Glans distinctly remote from apex of truncus; lateral sclerites bent towards each other and away from the truncus in distal half, its tips strongly ramified, touching each other; median plate very short, indistinct; stylus fairly stout, its tip bent towards the truncus.

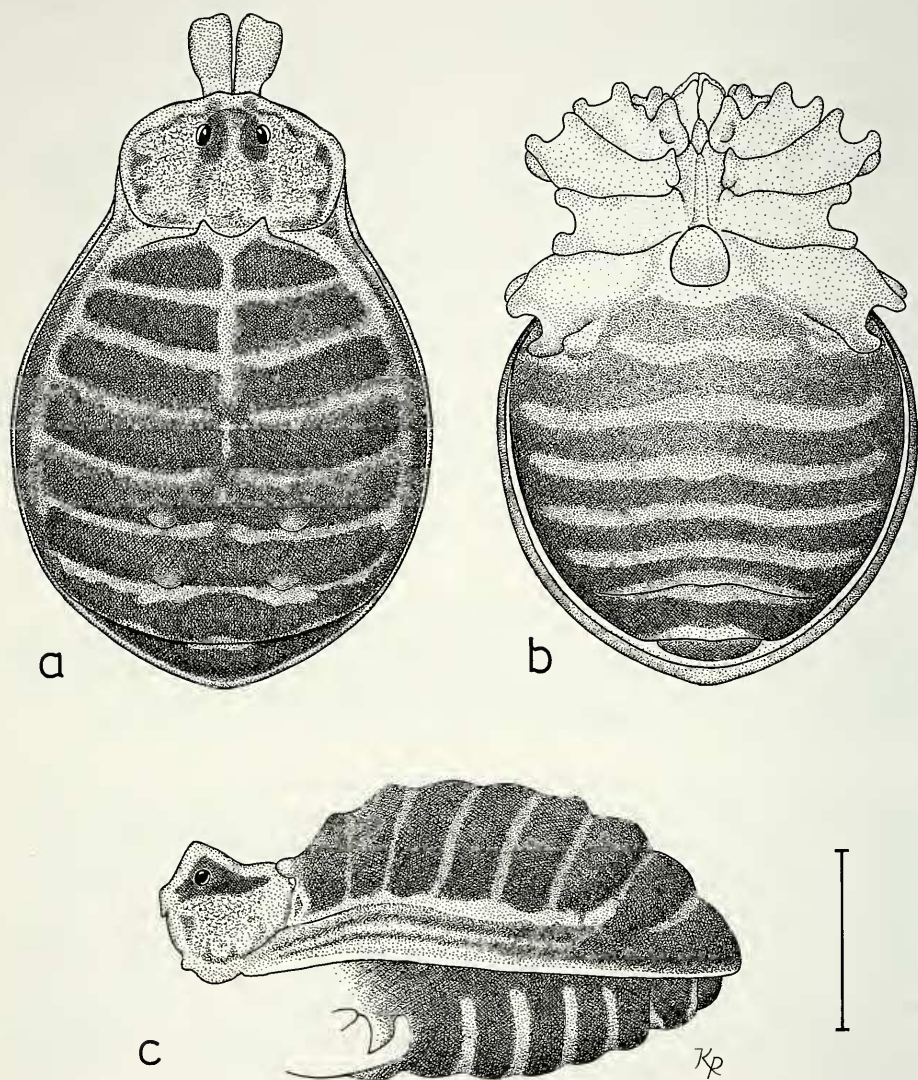


FIG. 104

Gnomulus leyteensis sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

♀. Unknown.

Measurements (♂): body 3.27 long, 2.39 wide; carapace region 0.76 long, 1.24 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.32	0.50	0.43	0.31	-	0.64	2.20
Leg I	0.27	0.85	0.53	0.56	0.87	0.55	3.63
Leg II	0.35	1.14	0.69	0.88	1.33	0.59	4.98
Leg III	0.31	0.87	0.58	0.64	1.11	0.46	3.97
Leg IV	0.41	1.19	0.72	0.96	1.59	0.50	5.37

Relationships: According to penis morphology *Gnomulus leyteensis* sp. n. is closest to *G. goodnighti*.

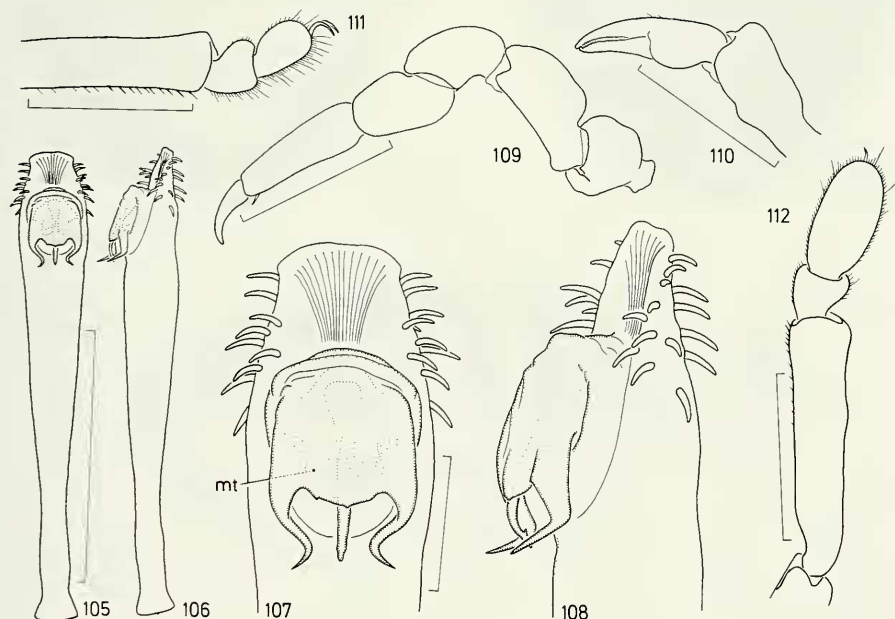
Bionomics: The specimen was sifted from leaf litter and humus on steep slopes of an evergreen primary forest. In small interspersed clearings bananas were grown.

Gnomulus laruticus sp. n.

Figs 105-113

Material: MALAYSIA, Perak, Taiping, Maxwell Hill (= Bukit Larut), 1320 m, ♂ holotype (MHNG), 26.I.1995, leg. P. Schwendinger.

Etymology: The species name is taken from Bukit Larut, the Malayan name of the type locality.



Figs 105-112

Gnomulus laruticus sp. n., holotype. - Penis, dorsal (105) and lateral view (106); apex of penis, dorsal (107) and lateral view (108); left palp, retrolateral view (109); left chelicera, retrolateral view (110); distal part of left leg IV, prolateral view (111) and of leg II, retrolateral view (112). - Scale lines 0.5 mm (105-106, 109-112), 0.1 mm (107-108).

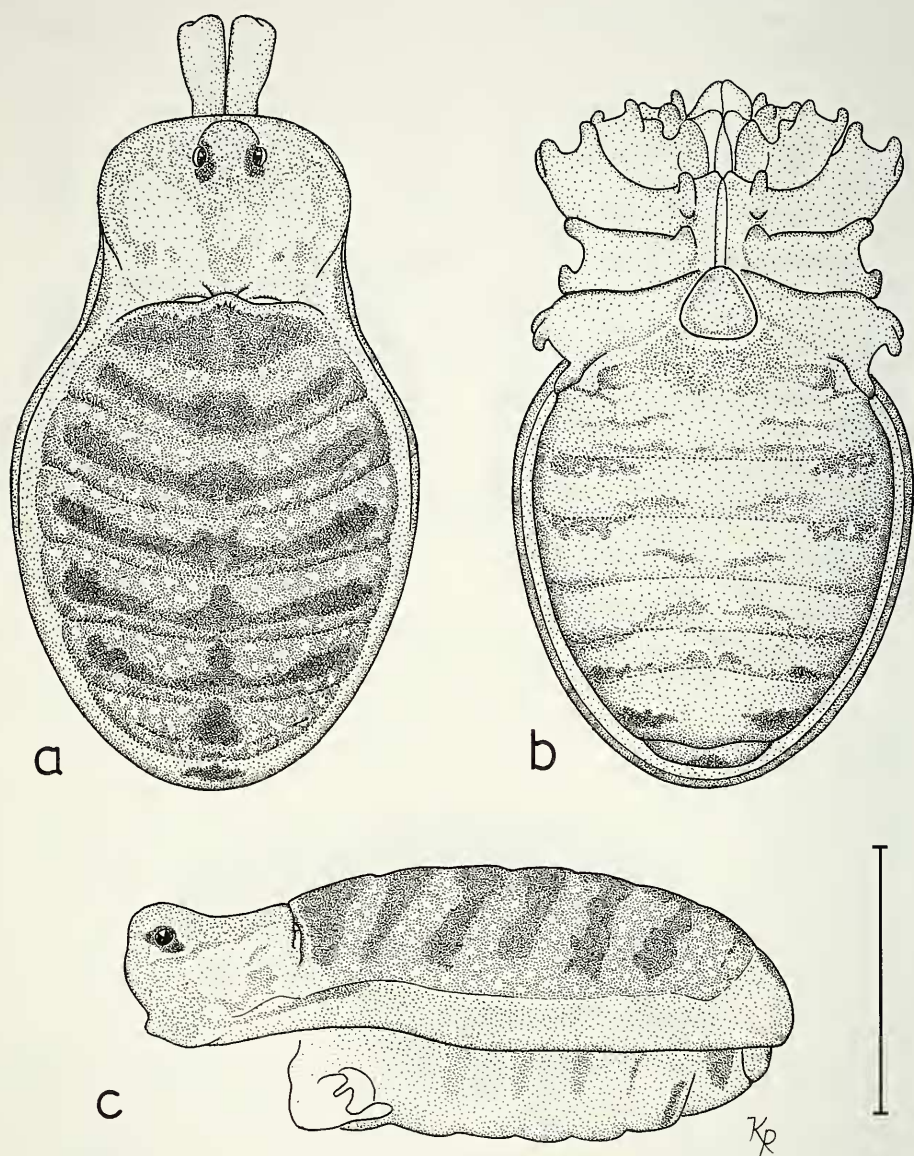


FIG. 113

Gnomulus laruticus sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Diagnosis: Resembling *G. crucifer* sp. n. in body shape and tarsal formula but different in shape of eye tubercle, colour pattern and presence of a wide bridge between carapace and abdominal part of dorsal scutum; genital operculum smaller; process on antero-lateral margin of leg coxae I present; ventral process on palpal trochanter smaller; low ventro-median hump on proximal article of chelicerae. Glans penis with slender stylus and pair of sigmoid, pointed lateral sclerites interconnected by a short, broadly rounded median plate (Figs 105-108).

Description: ♂ (holotype). Coloration: body mostly light amber. Dark reticulations on carapace and dark transversal bands on abdominal part of dorsal scutum (Fig. 113a); indistinct dark lateral and paramedian patches on ventral scutal areas (Fig. 113b). Femora to metatarsi of legs slightly darkened, metatarsus II and proximal half of tibia IV distinctly darkened.

Carapace with low, broadly rounded eye tubercle; posterior part of carapace slightly elevated; a single short, wide lobe there forming bridge with corresponding lobe (shorter, wider) on anterior margin of abdominal part of dorsal scutum (Figs 113a, c); dorsal and ventral scuta low, areas indistinctly elevated (Fig. 113c). Ventral leg coxa II with antero- and postero-proximal processes, coxa III with antero-proximal one; coxa I with conical process on antero-lateral margin; palpal coxa with ventral process; genital operculum subtriangular, wider than long (Figs. 113b).

Chelicerae (Fig. 110) weak; proximal article with dorso-distal boss and indistinct ventral process; hand slender.

Palps (Fig. 109): ventral femur with small proximal process; ventral trochanter with pronounced distad directed process.

Legs 3124 (Figs 111-112), tarsal formula 2-2-2-2.

Penis (Figs 105-108): truncus with narrow apex and broadly arched, medially indistinctly invaginated anterior margin; subapical setae in one group on each side. Glans with sigmoid lateral sclerites, their acutely pointed tips bent away from the truncus and away from each other. Median plate short, broadly rounded, with few tiny teeth on margin; pair of membranous tubes completely covered by median plate; stylus slender.

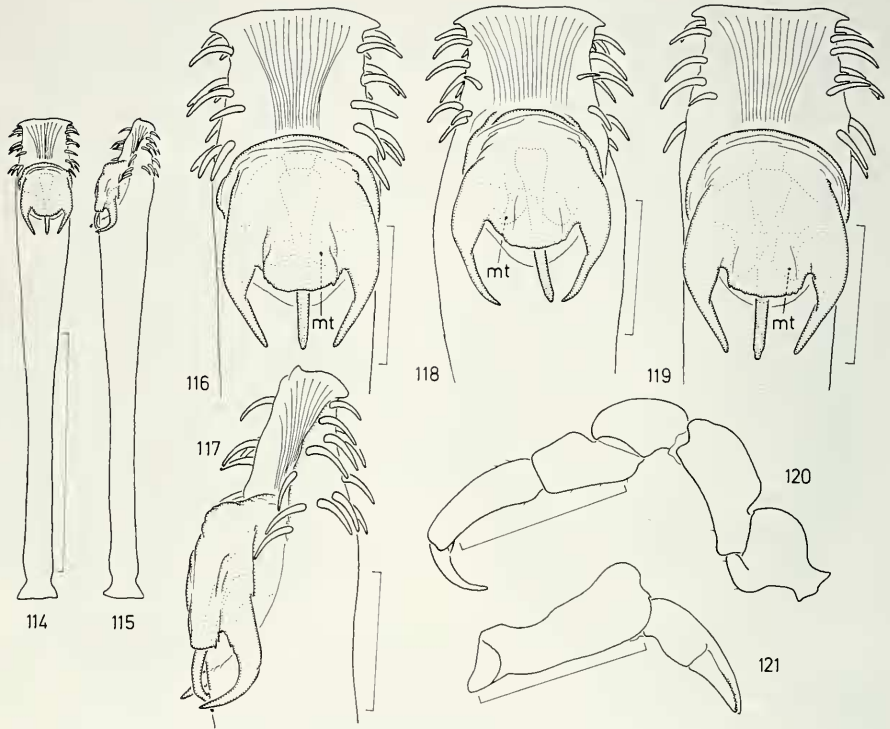
♀. Unknown.

Measurements (♂): body 2.48 long, 1.52 wide; carapace region 0.63 long, 0.94 wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.26	0.31	0.29	0.19	-	0.40	1.45
Leg I	0.23	0.66	0.40	0.35	0.53	0.37	2.54
Leg II	0.27	0.88	0.54	0.57	0.79	0.47	3.52
Leg III	0.23	0.56	0.40	0.38	0.64	0.27	2.48
Leg IV	0.26	0.86	0.55	0.63	0.92	0.31	3.53

Relationships: Congruences in penis morphology show closest relationship between *G. laruticus* sp. n., *G. asli* sp. n. and *G. hirsutus* sp. n. An unusual tarsal formula (2-2-2-2) links *G. laruticus* sp. n. with *G. crucifer* sp. n., but their distinctly different penes indicate a parallel retention of the juvenile tarsal number on posterior legs.

Bionomics: The specimen was collected by sifting leaf litter from the floor of a lower montane rain forest.



Figs 114-121

Gnomulus asli sp. n.: ♂ holotype (114-117), ♂ paratypes (118-119), ♀ paratype (120-121). - Penis, dorsal (114) and lateral view (115); apex of penis, dorsal (116, 118-119) and lateral view (117); left palp, retrolateral view (120); left chelicera, retrolateral view (121). - Scale lines 0.5 mm (114-115, 120-121), 0.1 mm (116-119).

Gnomulus asli sp. n.

Figs 114-122

Material: MALAYSIA, Perak, forest 5 km northeast of Chenderiang, 290-330 m, ♂ holotype (MHNG), 2 ♂, 1 ♀ paratypes (MAR, MHNG), 22.-31.I.1994; 330-400 m, 6 ♀ paratypes (MAR, MHNG), 15.-22.I.1995; leg. P. Schwendinger.

Etymology: Malay and Indonesian: *asli* = indigenous, original. The species is named after the Orang Asli, the indigenous people of Malaysia. The specimens were collected from a forest utilized by the inhabitants of an Orang Asli (Semai Senoi tribe) village.

Diagnosis: Close to *G. laruticus* sp. n. but distinguished by different colour pattern, lower eye tubercle, two bridge teeth between carapace and abdominal part of

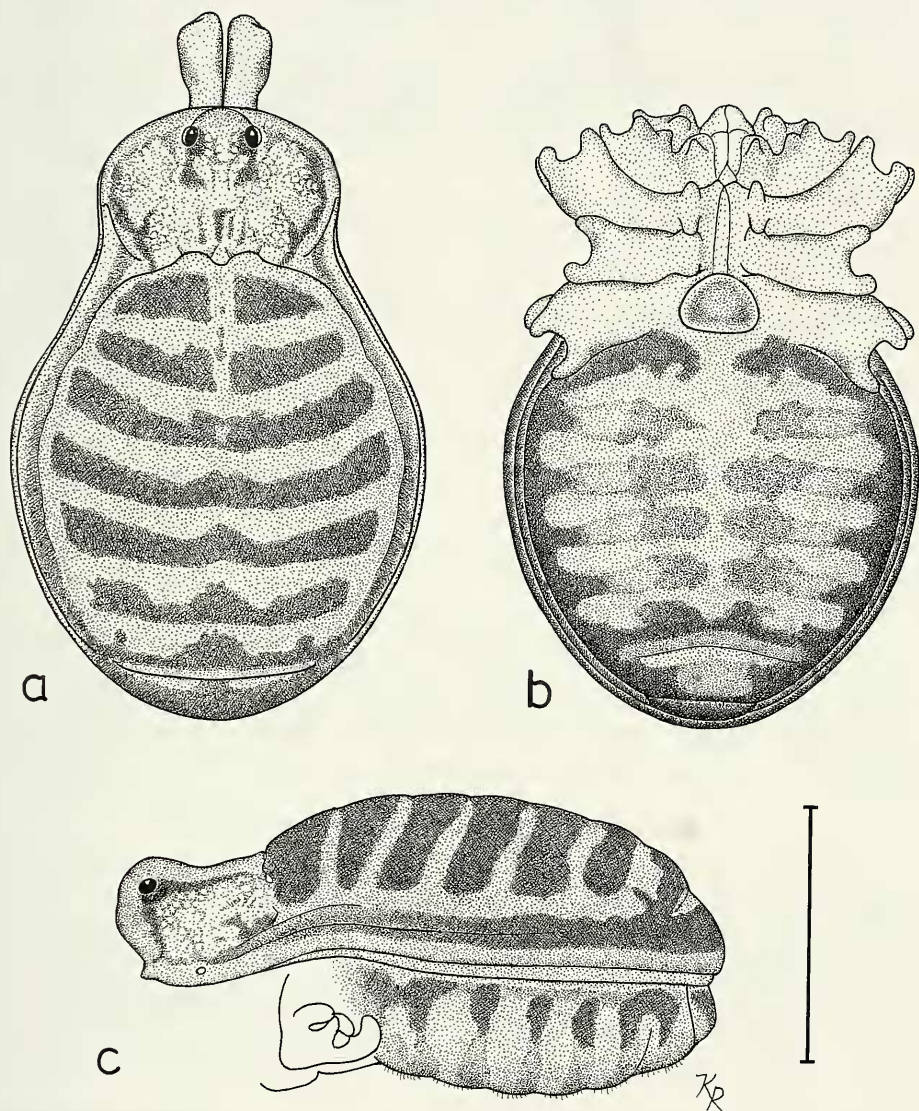


FIG. 122

Gnomulus asli sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

dorsal scutum, process on palpal trochanter basally rounded and tarsal formula 2-2-3-3. Glans penis distally wider; tips of lateral sclerites pointing towards each other (Figs 114-119).

Description: ♂ (holotype). Coloration: body mostly light amber, with dark reticulations on carapace and distinct dark transversal bands on abdominal part of dorsal scutum (Fig. 122a), indistinct ones on ventral scutum (Fig. 122b). Genital operculum and femora to metatarsi of legs dark amber, tarsi light yellow, ventral side of distitarsus I cream.

Carapace with low, broadly rounded eye tubercle; pars thoracica slightly elevated; two tubercles on posterior margin forming bridge with pair of short, obliquely truncate teeth on anterior margin of abdominal part of dorsal scutum (Fig. 122a, c); dorsal and ventral scuta low, areas indistinctly elevated; ventral scutal areas covered by fine short hairs (Fig. 122c). Ventral leg coxa II with distinct antero- and posterior-proximal processes, coxa III with antero-proximal one; coxa I with conical process on antero-lateral margin; palpal coxa with ventral process; genital operculum subtriangular, distinctly wider than long (Fig. 122b).

Chelicerae (Fig. 121) small, slender; proximal article with dorso-distal boss, no ventral process; hand slender.

Palps (Fig. 120): ventral femur with small proximal process; ventral trochanter with pronounced distad directed process.

Legs 1324, tarsal formula 2-2-3-3.

Penis (Figs 114-119): truncus slender, distal margin widely arched and indistinctly invaginated medially; subapical setae in one group on each side. Glans with sigmoid lateral sclerites, their pointed tips distinctly bent away from the truncus and towards each other. Median plate short, broadly rounded, with several denticles on margin; pair of membranous tubes completely covered by median plate; stylus slender.

♀. As the ♂, except for an indistinct hair cover on ventral scutum.

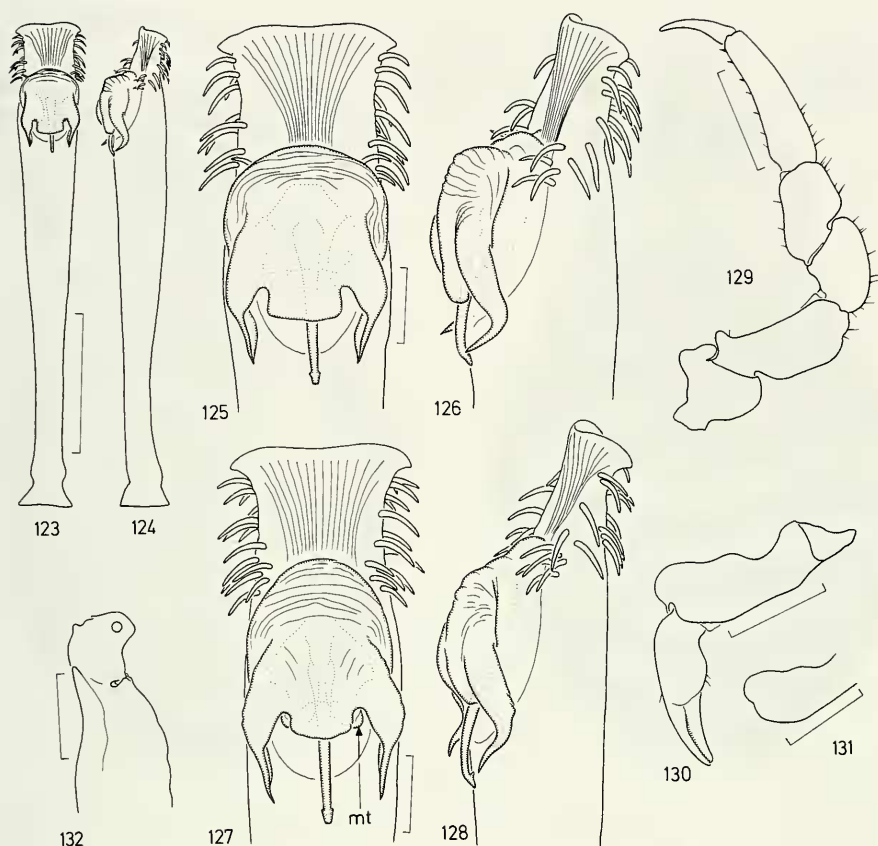
Measurements (♂, in brackets ♀): body 2.34 (2.39) long, 1.59 (1.63) wide; carapace region 0.61 (0.62) long, 0.92 (0.91) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.26 (0.27)	0.31 (0.31)	0.27 (0.27)	0.18 (0.18)	- -	0.38 (0.37)	1.40 (1.40)
Leg I	0.24 (0.24)	0.59 (0.60)	0.38 (0.37)	0.35 (0.34)	0.50 (0.50)	0.40 (0.40)	2.46 (2.45)
Leg II	0.29 (0.29)	0.81 (0.82)	0.47 (0.48)	0.50 (0.50)	0.79 (0.79)	0.48 (0.47)	3.34 (3.35)
Leg III	0.24 (0.24)	0.56 (0.56)	0.40 (0.38)	0.37 (0.37)	0.64 (0.64)	0.29 (0.29)	2.50 (2.48)
Leg IV	0.26 (0.27)	0.79 (0.79)	0.50 (0.50)	0.56 (0.56)	0.96 (0.96)	0.32 (0.32)	3.39 (3.40)

Variation: Body length/width ranges: ♂ 2.29-2.34/1.56-1.59 (n = 3), ♀ 2.28-2.51/1.51-1.69 (n = 7).

Relationships: Penis morphology shows that *G. asli* sp. n. and *G. laruticus* sp. n. are closest relatives, despite differences in the tarsal formula (2-2-3-3 versus 2-2-2-2) and in the shape of the carapace-abdomen bridge.

Bionomics: The specimens were sifted from leaf litter and humus in a lowland rain forest.



Figs 123-132

Gnomulus hirsutus sp. n.; ♂ holotype (123-126), ♂ paratype (127-128, 131-132), ♀ paratype (129-130). - Penis, dorsal (123) and lateral view (124); apex of penis, dorsal (125, 127) and lateral view (126, 128); left palp, retrolateral view (129); left chelicera, retrolateral view (130); left chelicera, proximal article, retrolateral view (131); anterior part of body, lateral view (132). - Scale lines 0.5 mm (123-124, 129-132), 0.1 mm (125-128).

Gnomulus hirsutus sp. n.

Figs 123-133

Material: MALAYSIA, Selangor, Templer Park, ♂ holotype and 1 ♀ paratype (MHNG), 1-3.XII.1990, leg. C. Deeleman-Reinhold. - Ulu Gombak, University of Malaya Field Centre, 200 m, 1 ♂, 1 ♀ paratypes (MAR, MHNG), 26.IX.1991, leg. D. Agosti. - Pahang, on the road to Genting Highlands, 500-800 m, 1 ♀ paratype (MAR), 13.XII.1982, leg. H. Ono.

Etymology: Latin: *hirsutus* = hairy; the specific epithet refers to the relatively hairy body of this species.

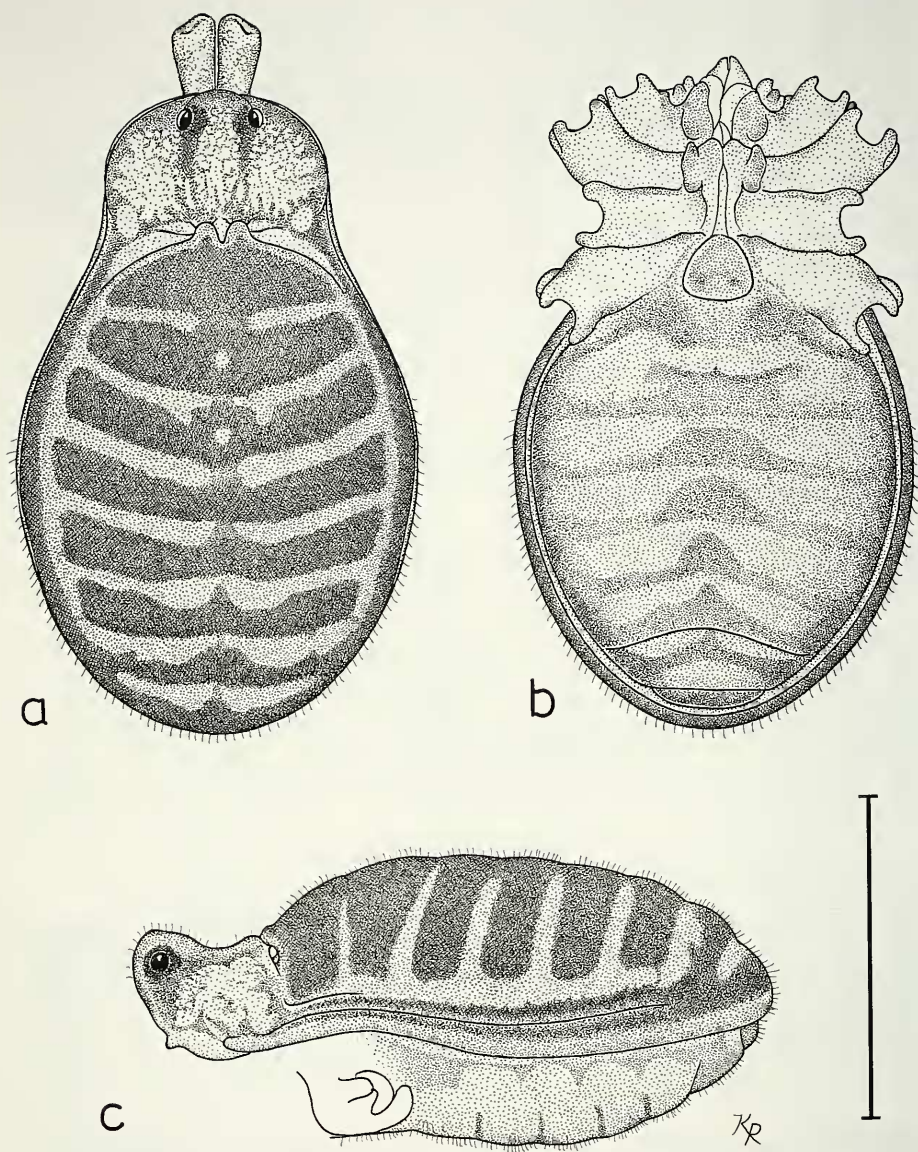


FIG. 133

Gnomulus hirsutus sp. n., ♂ holotype, body, dorsal (a), ventral (b) and lateral view (c). - Scale line 1 mm.

Diagnosis: Close to *G. asli* sp. n. but distinguished by larger body covered by fine hairs; eye tubercle higher, prorect; ventral scutal areas sexually dimorphic; ventral process on palpal trochanter basally narrower; proximal article of chelicerae with distinct dorso-median boss; glans penis with tips of lateral sclerites further apart from each other, median plate without marginal teeth (Figs 123-128).

Description: ♂ (holotype). Coloration: mostly dark amber, with dark reticulation on carapace, dark margin and transversal bands on abdominal part of dorsal scutum (Fig. 133a); ventral scutum light orange, its transversal bands indistinct (Fig. 133b); ventral prosoma light amber. Leg trochanters, chelicerae and pedipalps light yellow with dark spots (except on chelicerar hand and on palpal tarsus); leg tarsi light amber, ventral distitarsus I cream.

Whole body quite densely covered with fine light hairs. Carapace with prorect, rounded eye tubercle; pars thoracica only little elevated; two pairs of tubercles forming bridge between carapace and abdominal part of dorsal scutum; dorsal and ventral scuta low (Figs 133a, c); ventral scutal areas moderately swollen and pale (Figs 133b, c). Ventral leg coxa II with distinct antero- and postero-proximal processes overlapping antero-proximal process on coxa III; coxa I with central and antero-lateral processes; palpal coxa with ventral process; genital operculum broadly rounded anteriorly, slightly wider than long (Fig. 133b).

Chelicerae (Figs 130-131) weak; proximal article with distinct dorso-distal and smaller dorso-median boss, no ventral process; hand slender.

Palps (Fig. 129): ventral femur with distinct proximal process; ventral trochanter with pronounced distad-directed bilobed process.

Legs 1324, tarsal formula 2-2-3-3.

Penis (Figs 123-128): truncus slender, its distal margin broadly arched, indistinctly invaginated medially; subapical setae in one group on each side. Glans with sigmoid lateral sclerites, their pointed tips slightly bent away from the truncus and towards each other. Median plate short, without teeth on margin; pair of membranous tubes mostly covered by median plate; stylus slender.

♀. As the ♂, except for less elevated, more strongly pigmented ventral scutal areas.

Measurements (♂, in brackets ♀): body 4.02 (4.07) long, 2.54 (2.63) wide; carapace region 0.86 (0.83) long, 1.45 (1.41) wide. - Palp and legs:

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Palp	0.43 (0.43)	0.52 (0.50)	0.43 (0.43)	0.28 (0.29)	-	0.70 (0.66)	2.36 (2.31)
Leg I	0.43 (0.41)	0.96 (0.96)	0.59 (0.59)	0.56 (0.57)	0.78 (0.78)	0.61 (0.61)	3.93 (3.92)
Leg II	0.55 (0.53)	1.30 (1.33)	0.79 (0.81)	0.88 (0.88)	1.24 (1.25)	0.70 (0.70)	5.46 (5.50)
Leg III	0.42 (0.42)	0.93 (0.93)	0.64 (0.64)	0.61 (0.59)	1.02 (1.03)	0.47 (0.47)	4.09 (4.08)
Leg IV	0.50 (0.50)	1.36 (1.34)	0.82 (0.84)	0.95 (0.98)	1.55 (1.60)	0.55 (0.53)	5.73 (5.79)

Variation: Body length/width ranges: ♂ 3.81-4.02/2.54-2.57 (n = 2), ♀ 4.02-4.14/2.63-2.78 (n = 3). The ♀ from the type locality and the ♂ from Ulu Gombak have a more distinct dark pattern and a light longitudinal median stripe between areas II and III on their dorsal scutum. The ♀ from Ulu Gombak shows a faint pattern in the central region of its dorsal scutum. The ♂ paratype possesses an obliquely

truncate eye tubercle (as seen from laterally; Fig. 132), smaller bridge teeth on the anterior margin of its abdominal part of dorsal scutum and an indistinct dorso-median boss on the proximal article of its chelicerae (Fig. 131).

Relationships: External and genital morphology show closest relationship between *G. hirsutus* sp. n. and *G. asli* sp. n.; *G. laruticus* sp. n. is more distant. Another seemingly related form (only 1 ♀ available) occurs on Maxwell Hill.

Bionomics: The specimens were collected from leaf litter of primary and secondary evergreen forests.

UNDETERMINED MATERIAL

Nine other related forms are available only in ♀♀. We are reluctant to describe new species from ♀♀, since in the absence of penis characters a generic placement is by no means certain, considering the close external resemblance of *Palaeoncopus* gen. n. with *Caenoncopus* gen. n. and *Biantoncopus* gen. n. with *Gnomulus*. Nevertheless these specimens are recorded here, together with their presumed relationships, in the hope that further collecting at their find localities will yield ♂ specimens.

1. 1 ♀, Sumatra, 7 km north of Brastagi, 1500 m, 2.XII.1989, leg. I. Löbl *et al.* (MHNG) --- similar to *C. cuspidatus* (tarsi 1-1-2-2) but distinctly smaller; colour pattern different; interocular area not elevated; posterior margin of body more rounded; ventral process on palpal trochanter blunt. Collected from the same locality as *C. cuspidatus*, probably syntopic.
2. 1 ♀, Sumatra, Bukittinggi, Gunung Merapi, 2000-2200 m, 18.X.1990, leg. A. Riedel (MAR) --- similar to *C. tenuis* sp. n. but different in colour pattern, more slender legs and wider genital operculum.
3. 7 ♀, Sumatra, Mt. Kerinci, 1750-1900 m, 11.-13.XI.1989, leg. I. Löbl *et al.* (MHNG) --- close to *C. affinis* sp. n. but different in colour pattern; eye tubercle more rounded; genital operculum much larger; ventral process on palpal trochanter smaller.
4. 2 ♀, Sumatra, Panti, 250 m, 19.XI.1989, leg. I. Löbl *et al.* (MHNG) --- close to *P. gunung* sp. n. but distinctly smaller; eye tubercle and two humps on pars thoracica more elevated, the latter almost pointed. Apparently syntopic with *C. affinis* sp. n.
5. 1 ♀, Sumatra, Mt. Kerinci, 1750-1850 m, 11.-12.XI.1989, leg. I. Löbl *et al.* (MHNG) --- close to *P. gunung* sp. n. but much larger; pars thoracica lower, without pair of humps; ventral palpal trochanter with much larger, multilobed process; proximal article of chelicerae with pointed prodorsal process on distal corner.
6. 1 ♀, Indonesia, Kalimantan, Kaharian, 2.-16.IX.1985, leg. C. Deeleman-Reinhold (MAR) --- similar to *C. cuspidatus* (tarsi 1-1-2-2), but much larger; leg tarsi longer, more *Oncopus*-like; ventral process on palpal trochanter very long, bifurcate; chelicerae robust, proximal article with pointed prodorsal process on distal corner, second article with ventral process (as in *Oncopus* spp.). Judging from external morphology, this specimen appears intermediate between *Caenoncopus* gen. n. and *Oncopus*.

7. 1 ♀, Philippines, Leyte, Visca north of Baybay, 200-500 m, 23.II.1991, leg. J. Martens & W. Schawaller (MAR) --- similar to *B. fuscus* sp. n. (tarsi 2-2-3-3) but much larger; eye tubercle higher; ventral palpal trochanter and femur with conical processes; proximal article of chelicerae with erect dorso-median process. Syntopic with *G. leyteensis* sp. n.

8. 1 ♀, Philippines, Luzon, Sagada, 9.I.1980, leg. L. Deharveng (MAR) --- similar to *B. fuscus* sp. n. but distinctly larger; ventral process on palpal trochanter smaller. Syntopic with *G. maculatus* sp. n.

9. 1 ♀, Malaysia, Perak, Taiping, Maxwell Hill, ca. 1200 m, 10.IV.1990, leg. A. Riedel (MAR) --- similar to *G. hirsutus* sp. n. (tarsi 2-2-3-3) but smaller, less hairy and without distinct ventral process on proximal palpal femur. Distinct from *G. laruticus* sp. n., which occurs at the same locality.

DISCUSSION

GENITAL MORPHOLOGY

The description of *Caenoncopus cuspidatus* (SCHWENDINGER 1992) already showed that penis morphology in Oncopodidae is not as uniform as previously assumed and the new material uncovers even more complex conditions. At present, we can distinguish four major penis types. Three of them are characteristic for one genus each, the remaining one is shared by two genera.

Hypothetical ancestor. Our interpretation of phylogenetic relationships within the Oncopodidae is rooted in an ancestral penis type (Fig. 134a). Archaic Oncopodidae presumably possessed a cylindrical truncus and a short distad-directed glans with membraneous, slightly movable tubes. From this hypothetical form the four extant penis types may have evolved. These are:

Type 1. In the species of *Palaeoncopus* gen. n. the penis is structurally almost identical with the ancestral form (Fig. 134a), except for the lack of membraneous tubes (Fig. 134b).

Type 2. In *Biantoncopus* gen. n. (only known species *B. fuscus* sp. n.) the penis is similar to type 1, but stylus and membraneous tubes can be expanded by means of hemolymph pressure (Fig. 134c). During expansion the stylus is protruded distally and the membraneous tubes are bent to the opposite direction towards the base of the truncus. Structurally and functionally, this construction is very similar to other "hemolymph-pressure" lanitorean families (MARTENS 1986).

Type 3. The penes of *Gnomulus* and *Oncopus* possess the same elements as the hypothetical ancestor, but the whole glans is proximad-directed (Fig. 134d). This penis form was previously considered typical for the whole family (MARTENS 1976, 1986); it is found in the majority of species. A few of them, however, are already derived in that they have acquired an enlarged, prolonged "atypical" stylus (Fig. 134e: e.g. *G. maculatus* sp. n., *G. crucifer* sp. n.) and/or reduced the median plate (e.g. *G. leyteensis* sp. n., *G. crucifer* sp. n.).

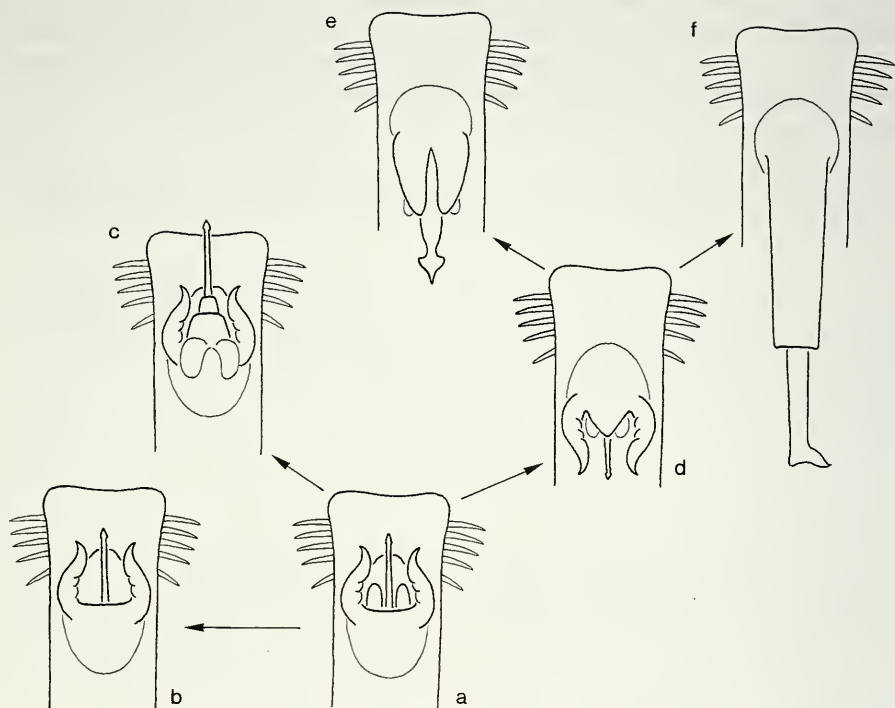


FIG. 134

Hypothetical evolution of the four penis types in Oncopodidae. - a) hypothetical ancestor with glans parts directed distad; b) type 1: *Palaeoncopus* gen. n., similar to state a), but membraneous tubes (see Fig. 1) lost; c) type 2: *Biantoncopus* gen. n. with parts of glans expandable; d) type 3: *Gnomulus* and *Oncopus*, glans bent proximad; e) *Gnomulus crucifer* sp. n., parts of the glans (especially stylus) noticeably elongated; f) type 4: *Caenoncopus* gen. n. with median plate and lateral sclerites reduced, stylus strongly elongated, embraced by proximal sheath. - This scheme does not reflect phylogenetic relationships, but shows trends in the evolution of penis types in Oncopodidae. *Caenoncopus* gen. n., for example, probably has not evolved directly from *Oncopus* or *Gnomulus*, but from a common ancestor with a penis as in d (see Discussion: Evolution).

Type 4. The penes of *Caenoncopus* gen. n. species are structurally unique and quite different from the other types. The truncus is dorso-ventrally depressed, its base not constricted and ending in two lobes. The glans essentially comprises only a very long, thick proximad-directed glans with an asymmetrical apex. Proximally, the stylus is embraced by a sheath-like membraneous collar formed by an extension of the membraneous socket; lateral sclerites, membraneous tubes and median plate are absent (Fig. 134f). This hypertrophic stylus is only partly homologous to the styli of the other penis types described above.

EVOLUTION

Our interpretation of taxonomic characters leads to the following possible evolutionary scenario. Primitive Oncopodidae were small (2-5 mm), sironoid-like opilionids, with large dorsal and ventral scuta, weak chelicerae and few leg tarsalia. The ancestral oncopodid penis was devoid of muscles and already characteristic for the derived group of "hemolymph-pressure" Laniatores. It had a short, distad-directed subapical glans with a free slender stylus surrounded by membraneous tubes and by lateral sclerites connected to a median plate (Fig. 134a). A similar penis morphology as presumed for early oncopodids is characteristic for two other families of "hemolymph-pressure" Laniatores, i.e. Gonyleptidae and Cosmetidae (MARTENS 1976, 1986). We take them as outgroup for our interpretation of relationships within the Oncopodidae. In these opilionids the subdistal glans is movable by means of hemolymph pressure only to a limited extent. As the stylus is pointing straight forwards, there is no need for a greatly movable glans. The penes of *Palaeoncopus gunung* sp. n., *P. kerdil* sp. n. and *P. katik* sp. n. from Sumatra largely accord with this primitive penis form, but are apomorphic in the loss of their membraneous glans tubes (Fig. 134b). *Biantoncopus fuscus* sp. n. from the Philippines also possesses a distad-directed glans penis (with membraneous tubes still present), but it has become expandable (Fig. 134c) in the same way as shown for the Biantidae (Martens 1978: figs 8a-e, 9a-d). The expanding stylus probably increases the insemination rate by enabling the ♂ to ejaculate deeper into the ♀ ovipositor.

From the primitive, generalized penis type with short distad-directed, non-expandable glans, the evolutionary trend in "hemolymph-pressure" Laniatores went towards enlargement and enhanced movability of the stylus. To keep the penis under the genital operculum and protect it from damage, it became necessary to either transpose the glans to a more proximal position on the truncus, or to retreat it deeply into the distal part of the truncus, or to fold it downwards. The latter option was realized in the majority of oncopodid species, the former ones in different lineages, i.e. in the Fissiphallidae, Assamiidae, Biantidae and Podoctidae (MARTENS 1986, 1988). After the glans became newly adjusted to a position with the stylus pointing to the truncus basis (Fig. 134d), evolution in Oncopodidae apparently went in two directions. *Caenoncopus* gen. spp. n. from Sumatra remained small, but greatly modified their penis morphology. In these species the lateral sclerites, median plate and membraneous tubes of the glans were lost, whereas the stylus gained enormous proportions and became asymmetrical (Fig. 134f). The rest of the Oncopodidae retained the typical penis structure (with short proximad-directed glans) but diversified in external characters instead. Most of them increased size of body and chelicerae (most pronounced in *Oncopus*) and acquired different tarsal formulas (2-2-2-2, 2-2-3-3 in *Gnomulus*, 1-1-1-1 in *Oncopus*). The evolutionary trend for stylus enlargement and reduction of glans sclerites, parallel to that in *Caenoncopus* gen. n., is also evident in the *Gnomulus-Oncopus* lineage, as shown in *G. maculatus* sp. n. (Figs 84-86) and *G. crucifer* sp. n. (Figs 73-75, 134e).

Divergent evolutionary lineages resulted in four distinctly different penis types, but specific distinctions within the same type are often minute. Considering

also the rapidly increasing number of newly discovered species with restricted distribution, it appears that the Oncopodidae currently undergo an active process of speciation. Unlike most other Laniatores, specific distinctions in Oncopodidae are expressed in penis modifications rather than in external morphology. Consequently, describing new taxa from ♀♀ or juveniles should be strictly avoided.

GENERIC LIMITS

Our reassessment of the Oncopodidae is primarily based on penis morphology, which is clearly outlined in the genera newly established in this paper. Only in *Gnomulus* penis shapes are fairly variable, with some species (e.g. *G. crucifer* sp. n.) being already as far derived from the usual type that they could be regarded as generically different. The penes of *Gnomulus* and *Oncopus*, on the other hand, are of the same type and no relevant distinctions could be found. Externally, however, *Oncopus* is clearly distinguished by its unique tarsal formula (1-1-1-1) and its robust body. Tarsal formulas, however, do not entirely correspond with genital characters used for generic distinctions. Different tarsal formulas exist in genera clearly defined by genital characters (1-1-2-2 and 1-1-3-3 in *Caenoncopus* gen. n.; 2-2-2-2 and 2-2-3-3 in *Gnomulus*) and the same tarsal formulas are present in different genera (1-1-3-3 in *Caenoncopus* gen. n. and *Palaeoncopus* gen. n., 2-2-3-3 in *Biantoncopus* gen. n. and *Gnomulus*). Consequently, the only reliable traits available at present to delineate genera within the Oncopodidae are genital characters.

The five oncopodid genera that we recognize here are founded on the following putative autapomorphies:

Palaeoncopus gen. n. - glans penis without membraneous tubes; palpal trochanter with prodorsal process.

Biantoncopus gen. n. - glans partly retreated into the distal part of the truncus, expandable by means of hemolymph pressure.

Gnomulus Thorell - glans proximad-directed. No relevant distinctions for *Pelitus* Thorell, therefore placed in synonymy with *Gnomulus*.

Oncopus Thorell - glans proximad-directed (but this is possibly synapomorphic with *Gnomulus*). Another possible autapomorphy is found in the strong chelicerae with 1-2 ventral processes on the cheliceral hand. At present, however, we cannot recognize any clear autapomorphies, which distinguish *Oncopus* from *Gnomulus*. External morphology (especially tarsal formula 1-1-1-1) is very characteristic for *Oncopus*, but it is not clear whether this (except for the large body size) is plesiomorphic or apomorphic.

Caenoncopus gen. n. - stylus strongly enlarged with membraneous collar and asymmetrical apex; other parts of glans lost.

FUNCTIONAL MORPHOLOGY OF THE ONCOPODID PENIS

The oncopodid penis operates by hemolymph pressure. Like in most other families of Laniatores, muscles and tendons are absent. Internal pressure of the body, transmitted to the penis via hemolymph, causes positioning of the glans in relation to

the truncus. Structure and alignment of the subdistal glans was previously regarded as fairly uniform. Only penis type 3 (Fig. 134d) was known and just a small degree of upward movement (less than 180°) by the short proximad-directed glans was thought to be possible (MARTENS 1986).

With the new material, greatly different conditions within the Oncopodidae are pointed out. Some of the new species exhibit penis forms with structural and functional characteristics as otherwise found only in different well-defined opilionid families (Fig. 134).

A similar short, distad-directed glans (considered plesiomorphic for the "hemolymph-pressure" Laniatores) as in *Palaeoncopus* gen. n. is present in Cosmetidae and Gonyleptidae. Within the primitive penis types derived forms can be identified, in which hemolymph pressure protrudes the stylus forward to reach the ♀ receptacula seminis more efficiently during copulation. Such is found in *Biantoncopus fuscus* sp. n., Assamiidae, Biantidae and Podoctidae. A short, proximad-directed glans, comparable to *Gnomulus* and *Oncopus*, is typical for many Phalangodidae, an obviously polyphyletic group. In separate evolutionary lineages the styli became increasingly enlarged. This occurs in the species of *Caenoncopus* gen. n. and, probably parallel to it, also in few *Gnomulus* species. Comparable hypertrophies of the stylus are present also in the family Triaenonychidae, where this phenomenon apparently evolved independently several times in different Australian and South American clades. In this family (belonging to Laniatores with a muscle-tendon complex inside the penis), the distad-directed stylus seems to be only slightly movable. In the cases mentioned, the stylus became a strongly elongated part of the truncus, but it was never folded downwards (HUNT & MAURY 1993).

The different penis types require modifications in mating behaviour. In this study, we did not examine the ovipositors of Oncopodidae in detail, but random samples showed that they are unsegmented, generally short and only movable to a small extent, if at all (MARTENS *et al.* 1981, observations from one *Oncopus* species). In terms of inner skeletal anatomy, the oncopodid ovipositor is very similar to that of other Laniatores.

In order to transfer sperm into the receptacula within the ovipositor, the ♂ needs to adjust his stylus to a suitable position by means of hemolymph pressure. This is done by slightly protruding the stylus in penis type 1 (Fig. 134b), or by inflating the membraneous tubes and strongly protruding the stylus in penis type 2 (Fig. 134c), or by folding the entire glans upwards about 180° (while only slightly protruding the stylus) in type 3 (Fig. 134d, e). It is not quite clear what happens during copulation in penis type 4 (Fig. 134f). Obviously the penis first has to be pushed out of the genital orifice for almost its entire length until the long stylus (Figs 5a, b, 9-10, 18-19) lies free and can be folded upwards. In *Caenoncopus cuspidatus*, with its glans only little shorter than the truncus, probably the maximum length of a proximad-directed glans is reached. To unfold this enormous sub-organ of the penis, the animal presumably has to rise high on its "tiptoes" and lift up its body quite a distance from the substrate. What movement these ♂♂ actually perform during mating can only be learned from observations on living animals.

ACKNOWLEDGEMENTS

We are grateful to Dr Bernd Hauser (MHNG) for his persistent incitement to take up this study and for the loan of specimens. Further material was kindly made available by the following colleagues: Dr Ben Brugge (ZMA), Dr Christa Deeleman-Reinhold (Sparrenlaan), Dr Louis Deharveng (Université Paul Sabatier, Toulouse), Dr Giuliano Doria (MCSNG), Dr Manfred Grasshoff (SMF), Dr Pekka Lehtinen (ZMT), Dr Ivan Löbl (MHNG), Dr Hirotugu Ono (National Science Museum, Tokyo), Mr Alexander Riedel (Zoologische Staatssammlung, München), Dr Wolfgang Schawaller (Staatliches Museum für Naturkunde, Stuttgart). Dr Konrad Thaler provided literature; Mr Konrad Eller, Mr Willi Salvenmoser and Mr Karl Schatz (all University of Innsbruck) helped producing SEM-micrographs. Dr J. Margraf (formerly Visca, Leyte) made a research stay of J.M. in Leyte, Philippines very successful. Mrs Käthe Rehbinder (Mainz) drew all whole-animal figures. Dr Stephen Elliott (Chiang Mai University) helped to improve the English text. The German Academic Exchange Service (Deutscher Akademischer Austauschdienst) supported P.S. with a research grant to work in Mainz for one month. The Feldbausch Foundation at "Fachbereich Biologie" of Mainz University granted travel funds to J.M. Our sincere thanks are due to all friends, colleagues and institutions mentioned.

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